REF
QK1
.A47573
v.53
1966
c.3

Volume 53 1966 Numbers 1-3

Annals of the Missouri Botanical Garden

Dates of Publication for Volume 53

No. 1, pp. 1-114, May 6, 1966

No. 2, pp. 115-264, November 7, 1966

No. 3, pp. 265-388, December 30, 1966

PUBLISHED BY THE BOARD OF TRUSTEES OF THE MISSOURI BOTANICAL GARDEN
AND WASHINGTON UNIVERSITY PRESS
ST. LOUIS, MISSOURI 63110

CONTENTS OF VOLUME 53

NUMBER 1

A contribution to the ecology of *Pelagophycus*,
by BRUCE C. PARKER and JOHN BLECK 1- 16

A preliminary ultrastructural study of the freshwater red alga *Compsopogon*,
by H. WAYNE NICHOLS, JOHN E. RIDGWAY and HAROLD C. BOLD 17- 27

Two new species of *Daphniphyllum*,
by TSENG-CHIENG HUANG 28- 31

The Asian genus *Neanotis* nomen novum (*Anotis*) and allied taxa in the Americas (*Rubiaceae*),
by WALTER H. LEWIS 32- 46

Revision of Mexican and Central American *Saurauia* (*Dilleniaceae*),
by GORDON E. HUNTER 47- 89

Two new species of *Chamaesyce* (*Euphorbiaceae*), new combinations, and a key to the Caribbean members of the genus,
by DEREK BURCH 91- 99

Chromosome numbers of phanerogams. 1 100-103

NOTES 104-114

New species of *Allomarkgrafia* and *Aspidosperma* (*Apocynaceae*) 104-105. A new species of *Platymiscium* (*Leguminosae*) from Panama 105. New species of *Coussarea, Machaonia,* and *Psychotria* (*Rubiaceae*) from Panama 105-109. *Hedyotis nicobarensis* Lewis, nom. nov. (*Rubiaceae*) 109. *Arcytophyllum laricifolium* (Cav.) Lewis, comb. nov. (*Rubiaceae*) 110. *Convolvulus rozynskii* (Standl.) Lewis & Oliver, comb. nov. (*Convolvulaceae*) 110. Two new species of *Gloeospermum* (*Violaceae*) from Panama 110-112. *Bernoullia* Oliv., a genus of *Bombacaceae* new to Panama 112-113. The publication date of the genus *Cochlospermum* (*Cochlospermaceae*) 113. *Pavonia* (*Peltaea*) *trinervis* (Presl) A. Robyns, comb. nov. (*Malvaceae*) 113-114. *Hibiscus luteus* (Rolfe) L. O. Williams & A. Robyns, comb. nov. (*Malvaceae*) 114.

NUMBER 2

Revision of the North and Central American hexandrous species of *Aristolochia* (*Aristolochiaceae*),
by HOWARD W. PFEIFER 115-196

The genus *Erythronium* (*Liliaceae*) in Kansas,
by KENNETH R. ROBERTSON 197-204

Taxonomic status of *Claytonia rosea* and *C. lanceolata* (*Portulacaceae*),
by DIANNE K. HALLECK and DELBERT WIENS 205-212

Pollen morphology and classification of the *Pyrolaceae* and *Monotropaceae*,
by JOAN W. NOWICKE 213-219

Systematic implications from electron microscopic studies of *Compositae* pollen—a review,
by JOHN J. SKVARLA and B. L. TURNER 220-256

NOTES 257-264

Chromosome numbers of *Oldenlandia corymbosa* (*Rubiaceae*) from southeastern Asia 257-258. *Claytonia caroliniana* var. *spatulifolia* (Salisbury) Lewis, stat. nov. (*Portulacaceae*) 258-259. Addendum: Schlechter's New Guinea duplicates of *Liparis* (*Orchidaceae*) at the Missouri Botanical Garden 259-260. *Mesechites pilosissima* Woodson (*Apocynaceae*) new to Peru 260-261. *Piper* and *Peperomia* (*Piperaceae*) new to Panama 261-264. Photographs of African type collections 264.

NUMBER 3

Central American and West Indian species of *Inga* (*Leguminosae*),
by JORGE LEÓN 265-359

Dukea, a new genus of the *Rubiaceae* (Tribe *Mussaendeae*),
by JOHN D. DWYER 360-367

Notes on *Coussarea* (*Rubiaceae*), especially the Panamanian species, by JOHN D. DWYER and SISTER M. VICTORIA HAYDEN.................................368-374

NOTES 375-384

The genus *Poinsettia* (*Euphorbiaceae*) in Florida 375-376. *Ilex discolor* var. *lamprophylla* (Standl.) Edwin, stat. nov. (*Aquifoliaceae*) 376. A new species of *Inga* (*Leguminosae*) from Panama 377. Typification of *Hedyotis procumbens* (*Rubiaceae*) and a new variety from southeastern United States 377-378. Three lost species of *Piper* (*Piperaceae*) 378-379. New *Piperaceae* from Ecuador 379-381. New species of *Piper* and *Peperomia* (*Piperaceae*) from Peru 381-384.

General Index for Volume 53, 1966...385-388

ERRATA

Page 33, line 41. For *A. filiformis* read *A. conferta.*

Page 102, line 20. For 6542 read 6572.

Page 371, table 2, footnote 1. For Styles read Stipules.

Volume 53 1966 No. 1

Annals
of the
Missouri Botanical Garden

The previous issue of the ANNALS OF THE MISSOURI BOTANICAL GARDEN, Vol. 52, No. 4, pp. 487-604, was published on January 5, 1966.

PUBLISHED BY THE BOARD OF TRUSTEES OF THE MISSOURI BOTANICAL GARDEN
AND WASHINGTON UNIVERSITY PRESS
ST. LOUIS, MISSOURI 63110

Annals
of the
Missouri Botanical Garden

A journal containing scientific contributions from the Missouri Botanical Garden and the Department of Botany of Washington University in affiliation with the Missouri Botanical Garden.

EDITORIAL COMMITTEE

WALTER H. LEWIS, *Editor*
Missouri Botanical Garden & Washington University

JOHN D. DWYER, *Missouri Botanical Garden & St. Louis University*
H. WAYNE NICHOLS, *Missouri Botanical Garden & Washington University*
ANDRÉ ROBYNS, *Missouri Botanical Garden & Washington University*
GEORGE B. VAN SCHAACK, *Missouri Botanical Garden*

Information

THE ANNALS OF THE MISSOURI BOTANICAL GARDEN appears three times during the calendar year. Three numbers totaling about 400 pages constitute a volume.

Beginning with Volume 53, 1966:

Subscription Price	$15.00 per volume
Single Numbers	5.50 each

Contents of previous issues of the ANNALS OF THE MISSOURI BOTANICAL GARDEN are listed in the Agricultural Index, published by the H. W. Wilson Company.

Beginning June 1, 1962 the Stechert-Hafner Service Agency, Inc., 31 East 10th St., New York 3, N. Y., became sole agent for the ANNALS OF THE MISSOURI BOTANICAL GARDEN. The Agency handles all subscriptions, all claims beginning with volume 50 (1963) and all requests for back issues. Out-of-print numbers will be reprinted as may be required.

Under the arrangement with the Stechert-Hafner Service Agency, the Agency handles also all purchases of any portion of the ANNALS subseries known as the "Flora of Panama."

All matters regarding exchange continue to be handled by the Missouri Botanical Garden as in the past.

Printed by the Eden Publishing House, St. Louis, Missouri, 63103.

Annals
of the
Missouri Botanical Garden

Vol. 53 | 1966 | No. 1

A CONTRIBUTION TO THE ECOLOGY OF PELAGOPHYCUS[1]

BY BRUCE C. PARKER AND JOHN BLECK

Department of Botany, Washington University, St. Louis, Missouri and
Department of Botany & Plant Biochemistry, University of California, Los Angeles

ABSTRACT

A year-round study of the giant benthic kelp, *Pelagophycus giganteus,* was conducted by scuba diving. Several lines of evidence, including laboratory studies, point to a seasonal temperature-regulated sexual life-cycle for this essentially annual species. Juvenile sporophytes grow faster and have a higher mortality rate than adult, reproductive plants. Most members of he population develop at 70-100 ft depth which receives 5-10% of the surface blue-green illumination, but adult plants at the population's outer periphery (125 ft deep) receive less than 1% of the surface blue-green illumination. Juvenile transplants of the close relative, *P. porra*, do not develop in the natural habitat of *P. giganteus.*

Pelagophycus is a giant lessoniaceous brown alga endemic to the islands and coastal waters of southern California and northern Baja California. Until recently little was known of this relatively inaccessible, deep-water kelp. However, the improvement of scuba diving techniques and increased interest in ocean resources have enabled and encouraged more extensive investigations of this alga in its natural habitat.

Dawson (1962), Parker & Dawson (1964), and Parker & Bleck (1965) studied the systematics and distribution of the three species of *Pelagophycus*. Parker & Fu (1965) compared the anatomy of *P. giganteus* to that of *P. porra* and to *Macrocystis* and *Nereocystis*. Parker & Dawson (1965) described a fossil Miocene kelp from southern California which appears intermediate between *Pelagophycus* and *Nereocystis*. Thus, while the taxonomy and structure of mature, reproductive plants of this genus have been treated, practically no information is available concerning the growth and development of the sporophytic generation. Further, the life-cycle, beyond that reported for *P. porra* by Herbst & Johnstone (1937), is poorly known. Studies along these lines provide a basis for understanding the ecology of

[1] This study was supported, in part, by a grant from the University of California, Los Angeles; we also wish to acknowledge the indispensable assistance of Frances Sizelove of the Glendale Y.M.C.A. and numerous scuba divers of the U.C.L.A. senior diving team.

ANN. MISSOURI BOT. GARD. **53**(1): 1-16, 1966.

The previous issue of the ANNALS OF THE MISSOURI BOTANICAL GARDEN, Vol. **52**, No. 4, pp. 487-604, was published on January 5, 1966.

Pelagophycus, including the longevity of plants, factors affecting distribution limits of the species, and stability of morphological features now used as taxonomic criteria for the species.

The population of *P. giganteus* at Long Point, Santa Catalina Island, California, was selected for these studies because the location (10 mi by land + 20 mi by sea) was the nearest known, undisturbed habitat of *Pelagophycus* to the investigators' laboratory at the University of California, Los Angeles. The objectives of this investigation were designed to meet the limits imposed by (a) distance and sea travel facilities, as influenced by weather conditions, to and from the experimental site, (b) availability of scuba diver personnel, (c) maximum allowable time per diver at a depth of 90 ft, (d) scuba diver proficiency in terms of physical dexterity for measuring and recording data in the natural environment of *Pelagophycus*. With these limitations in mind, we set the following specific goals:

1. To establish two 12 × 50 ft rectangular, submarine plots, tag the plants therein, and make periodic measurements of stipe length, maximum pneumatocyst width, and maximum holdfast diameter in parallel with observations of sporophyte plant development.
2. To measure temperature and light, as time and equipment permitted, at the experimental site during the course of other operations.
3. To transplant juvenile sporophytes of *P. porra* from their coastal habitat to the natural insular habitat of *P. giganteus* at Long Point, Santa Catalina Island, and follow their growth and development.
4. To culture spores of *P. giganteus* and follow their development as a supplement to observations of macroscopic sporophyte development in the natural environment.

We estimated that the above objectives might be accomplished within 1½ years.

PRELIMINARY STUDIES AND ESTABLISHMENT OF EXPERIMENTAL PLOTS

We obtained transportation and accommodations chiefly from the Glendale, California Y.M.C.A. which maintains a camp at Long Point and operates a 35 ft supply boat to and from the camp site periodically on a year-round basis. Initially two-day visits were planned at least once each month, and on occasions, we had to travel by seaplane or commercial boat to Avalon, Santa Catalina Island, then proceed by special charter boat to Long Point. One of us (J. B.) participated in all dives and directed the submarine operations. A few to many volunteer divers assisted in initiating experiments and collecting data.

Following exploratory dives to evaluate the size and density of the population on February 1, 1964, the two rectangular plots (12 × 50 ft) were demarcated with 12 ft aluminum rods and 50 ft nylon lines; the latter was secured by metal corner stakes. An air-filled, white plastic bottle attached to one corner served as a marker for quick location of plots during subsequent dives. The plots were intentionally established near the center of the *Pelagophycus* population and encompassed about

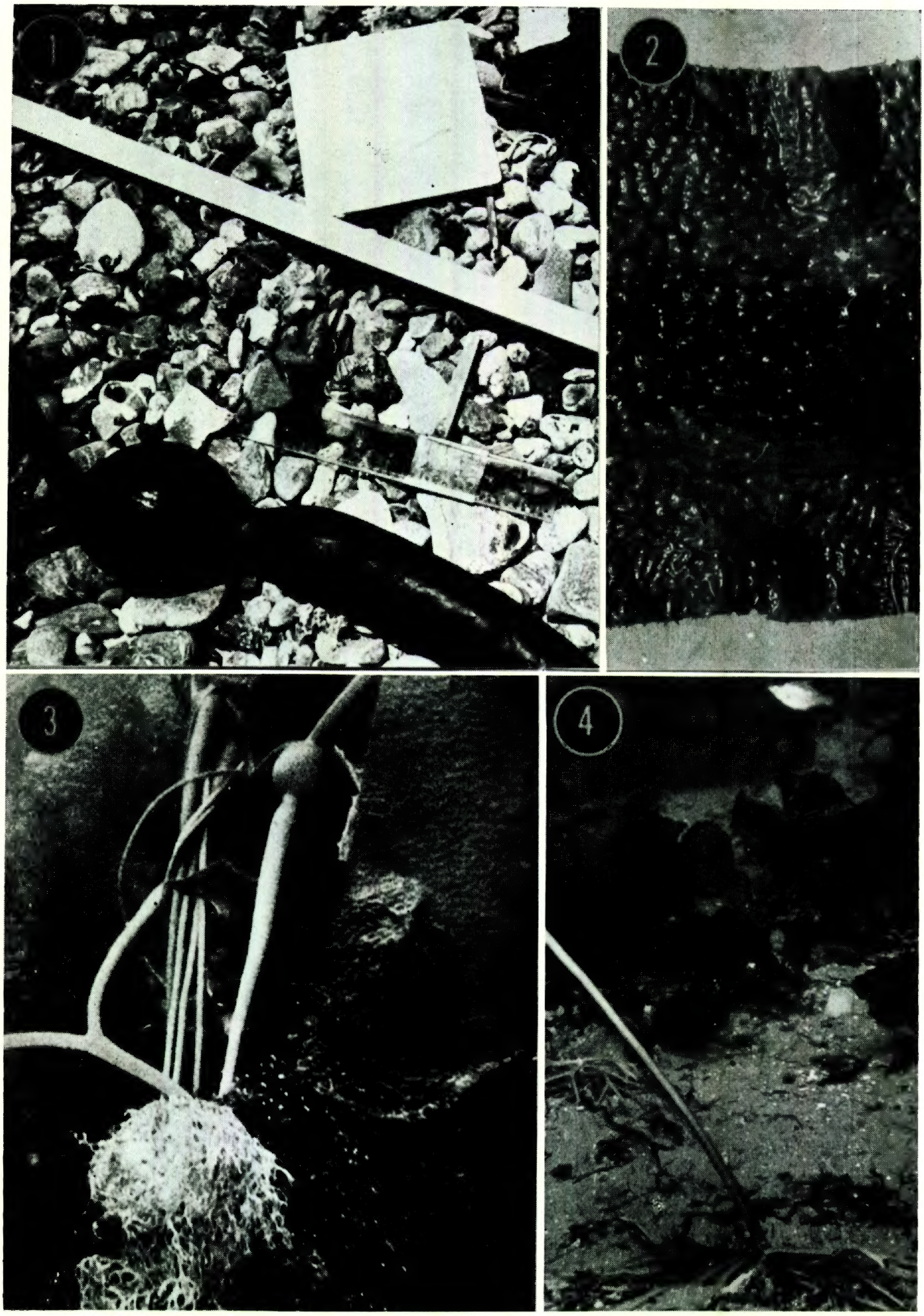


Fig. 1. On Long Point beach, from upper right to lower left: Scuba recording slate and pencil, portion of meter rule for stipe measurements, calipers for pneumatocyst measurements, pneumatocyst and adjacent parts of mature *P. giganteus;* ×0.2. Fig. 2. Portion of fertile blade of *P. giganteus* showing darker sorus running the length of the blade; ×0.12. Fig. 3. Groups of entangled *P. giganteus* at ca 90 ft depth at Long Point. Shows dislodged holdfasts, five or more stipes, a pneumatocyst, antlers, and portions of blades; ca ×0.07. Fig. 4. Holdfast and lower stipe of *P. giganteus* at ca 90 ft depth; ×0.1.

the same number of plants as found in an equivalent area elsewhere in the population (i.e. ca 8 adults/600 sq ft). Plot 1 occurred at 80-85 ft depth, while Plot 2 was located at a depth of 85-90 ft. *Pelagophycus* sporophytes within these plots received a numbered, yellow, plastic tag (ca 1.5 × 3 in) attached with plastic-covered wire just above the pneumatocyst (Fig. 1, 3, 5). In this and all later operations, the divers avoided excessive disturbance of plants and substratum.

The exploratory dives revealed that the entire population of *P. giganteus* at Long Point stretched across the cove for several hundred yards. Occasional plants occurred at about 50 ft and the population continued to a depth of at least 125 ft. These inner and outer boundaries of the population reached a horizontal distance of about 225-300 ft. *P. giganteus* possesses a large flattened holdfast partially buried in the substratum of grey silty sand (Fig. 4). Occasional outcroppings of rocky reefs interrupted the population of *P. giganteus*. The rocks contained a denser community of plants and animals, *Macrocystis pyrifera* being one of the dominants. The less dense *P. giganteus* community contained such seaweeds as *Dictyopteris* sp., *Eisenia arborea* Areschoug, *Laminaria farlowii* Setchell, *Ectocarpus* sp., and several red algae encrusting small pebbles. Some animals frequently observed were *Astraea undosa* (wavy top snail), *Conus californicus* (California cone snail), *Norrisia norrisii* (smooth turban snail), *Tegula aureotincta* (guilded turban snail), *Stichopus parvimensis* (sea cucumber), one or more species of tube anemone (*Ceriantheridae*), *Chromis punctipinuis* (blacksmith fish), *Oxyjulis californica* (Senorita fish), *Paralabrax clathratus* (kelp bass). Some of the larger game fishes *Paralicthys californicus* (halibut) and *Pimelometapon pulcrum* (sheepshead) sometimes lay beneath the massive 35 ft-long blades of *Pelagophycus*. These blades characteristically extended horizontally in the direction of the prevailing current with their distal two-thirds drooping close to the substratum (Fig. 3, 5). The light beneath these blades was drastically reduced.

During our first observations of *Pelagophycus* at Long Point in the late summer and fall of 1963, we rarely encountered juvenile sporophytic plants. Juveniles were still scarce on February 1-2, 1964, which explains why the nine tagged plants in Plot 1 and six tagged specimens in Plot 2 were mature, judging from their blade numbers and other morphological features. One outstanding difference between plants observed on February 1-2, 1964, and those observed and collected during 1963, was the occurrence of reproductive sori on most of the blades of the February plants (Fig. 2).

Measurements of Growth and Development

Initial measurements of tagged plants were made February 8, 1964. Measurements were taken subsequently at approximately 5-week intervals until June 16, 1965, when the study was terminated. Stipe length was determined with a meter rule to the nearest centimeter, while maximum pneumatocyst diameter was determined with calipers (Fig. 1). Measurements by different divers on identical plants within a few minutes of each other never varied by more than 2.8 cm for stipe length, nor more than 0.4 cm for pneumatocyst width. These proved the most reliable measureable features of these giant seaweeds. Blades were too delicate to

be manipulated by divers, and holdfasts, which were initially included in the measurements, proved unreliable due to periodic shifting of the sandy substratum which exposed or covered parts of this organ. All measurements and other observations were promptly recorded on a slate carried by each diver (Fig. 1).

At the time of tagging, plants 3 and 5 in Plot 1 possessed four blades each, while plant 6 had five blades and the remaining individuals had six blades each. All Plot 1 plants had elliptical pneumatocysts (Fig. 1, 5) except No. 2 which had a relatively spherical one (Fig. 3). In Plot 2, plant No. 4 had four blades, Nos. 1 and 5 had five blades each, Nos. 2 and 6 had six blades, and No. 3 had seven blades. All Plot 2 plants had elliptical pneumatocysts except Nos. 2 and 3. Throughout these studies, the numbers of blades on these plants did not change except in the case of Nos. 1 and 5 in Plot 2 which ultimately developed six blades each. The observed initial shape of the pneumatocyst of all tagged plants did not change.

Table 1 contains the data for stipe length and maximum pneumatocyst width. Note that all plants in Plot 1, except No. 9, disappeared within seven months of their initial tagging, while the majority of plants in Plot 2 persisted for more than a year. On June 16, 1965, our last visit to the plots still revealed plants 1 and 2, thus constituting 16½ months from the time of their initial tagging.

The mean increments for the intervals in Table 1 do not represent significant values for the whole population of *P. giganteus* at Long Point. These values, however, indicate the general trends in stipe elongation and pneumatocyst enlargement for mature plants in the plots. The mean increase in stipe length per plant during the entire period of 16 months is approximately 15 cm suggesting an average rate of stipe elongation of nearly 1 cm per month. For the pneumatocyst, the mean increase in maximum width is approximately 0.18 cm which constitutes an average rate of enlargement of 0.01 cm per month.

Some values in Table 1 appear discrepant because they represent decreases in stipe length or pneumatocyst width in excess of that which would be expected to occur through measurement errors. Examples of these and dates of measurement for Plot 1 are, as follows: Plant No. 1 (5-2-64 and 8-2-64), No. 3 (8-2-64), No. 5 (3-28-64), all pertaining to stipe length; No. 9 (5-2-64 and 10-11-64) pertaining to pneumatocyst width. Examples of discrepant figures in Plot 2 are, as follows: Plant No. 4 (5-2-64), No. 5 (6-10-64 and 1-16-65), No. 6 (8-2-64), all pertaining to stipe length; No. 2 (6-10-64), No. 4 (3-28-64 and 6-10-64), No. 5 (1-16-65 and 2-13-65), pertaining to pneumatocyst width.

With respect to stipe length discrepancies, we found that haptera originate continuously through the life of a mature plant. They are produced at the base of the stipe just above the level of the last-formed haptera. Our stipe length measurements include the distance between the uppermost haptera of the holdfast and the pneumatocyst base. Thus, these apparent reductions in stipe length are results of haptera production, and the elongation rates of the stipes as recorded in our tables are probably slightly less than the actual rate of stipe elongation. We were unable to find a reason for the discrepancies in pneumatocyst measurements although the possibility of different gas pressures within this organ has occurred to us.

Table 1. Measurements of stipe elongation and pneumatocyst width expansion (in parentheses) for *Pelagophycus giganteus* adult plants in plots 1 and 2 (all in cm.).

Date	PLOT 1									PLOT 2						Mean Incre-ments
	Plant no.									Plant no.						
	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	
2-8-64	117 (8.57)	162 (9.30)	200 (7.32)	205 (8.57)	200 (7.62)	210 (8.57)	230 (7.92)	275 (8.57)	132 (7.32)	150 (7.92)	148 (7.92)	154 (8.89)	115 (8.57)	76 (8.25)	90 (7.62)	
3-28-64	120 (8.89)	Gone	200 (7.62)	Gone	190 (8.08)	200 (8.57)	230 (8.57)	275 (8.89)	130 (8.08)	160 (8.41)	155 (8.41)	155 (9.30)	120 (8.08)	75 (8.08)	90 (8.25)	0.23 (0.40)
5-2-64	106 (8.89)		220 (7.62)		190 (7.92)	Gone	230 (8.57)	285 (8.57)	140 (7.62)	160 (8.25)	158 (9.30)	160 (9.19)	110 (8.89)	78 (8.25)	95 (8.89)	2.7 (0.11)
6-10-64	115 (9.04)		225 (7.92)		210 (7.92)		235 (8.57)	300 (9.19)	140 (8.57)	180 (8.89)	170 (8.73)	160 (9.19)	120 (8.57)	70 (8.25)	95 (8.89)	7.3 (0.23)
8-2-64	108 (8.89)		215 (8.25)		215 (8.25)		230 (8.57)	* (9.30)	142 (8.57)	180 (8.89)	175 (9.86)	160 (9.19)	Gone	75 (8.57)	90 (9.19)	—1.0 (0.12)
9-12-64	Gone		Gone		Gone		Gone	Gone	142 (9.19)	187 (9.19)	178 (8.89)	157 (9.30)		77 (8.57)	100 (9.30)	3.2 (0.03)
10-11-64									144 (8.57)	—	180 (9.19)	157 (9.30)		76 (8.89)	100 (9.86)	0.6 (0.13)
11-28-64									140 (8.57)	197 (9.30)	183 (9.19)	161 (9.19)		80 (8.89)	100 (0.16)	2.9 (0.05)
1-16-65									Gone	200 (9.30)	180 (9.19)	161 (9.30)		74 (8.57)	98 (9.86)	—1.6 (—.10)
2-1-65										195 (9.30)	178 (9.19)	158 (9.30)		75 (8.89)	100 (10.16)	—1.4 (0.12)
2-13-65										194 (9.30)	178 (9.19)	160 (9.30)		73 (8.57)	100 (10.16)	0.33 (—.06)
3-20-65										199 (9.30)	176 (9.19)	—		74 (8.57)	100 (10.16)	1.0 (0)
4-24-65										195 (—)	—	158 (—)		74 (—)	Gone	—2.0 (—)
6-16-65										197 (10.16)	178 (9.19)	Gone		Gone		2.5 (0.43)

*Plant dislodged by diver during pneumatocyst measurement.

Sori were abundant on blades of all plants within plots from the beginning of our study in February, 1964, until September, when an obvious reduction in soral area on blades was noted. No juvenile plants occurred inside or in the vicinity of the plots until May 2, 1964, when tiny, barely visible brown algae, presumed to be *Pelagophycus,* made a dramatic appearance. Each plot contained nearly 1000 of these plants. On June 10, 1964, we confirmed the identity of many of these plants which had formed pneumatocysts and antlers characteristic of the genus. Plants were too small and delicate to be tagged and measured during this early stage of development, but we noted that a high percentage of the juveniles had already disappeared. In October, all juveniles remaining in the plots were tagged and measured.

The data for stipe length and pneumatocyst width of the juvenile plants in the plots are recorded in Table 2. Note that only two of the seven tagged juveniles survived until June 16, 1965. Because their origin as macroscopic sporophytes was approximately May 2, 1964, these two remaining plants were approximately one year old. A comparison of the Mean Increments of these plants in Table 2 with those for the mature plants in Table 1 shows that the stipes and pneumatocysts of the juveniles elongated and expanded more rapidly than those of the adult plants. On the average, the stipes of the juvenile plants elongated approximately 10-11 cm per month.

Because we had found so few juveniles in our plots, we sought further data from juveniles by making a 100 ft line transect a few feet north of the two plots. All *Pelagophycus* individuals with holdfasts less than one foot on either side of this line received numbered tags. Measurements were taken, as described previously. The data on stipe elongation and pneumatocyst enlargement for 20 plants along this line transect are recorded in Table 2. These 20 plants perhaps constitute a more heterogeneous sample than the ones located in the plots, because of greater differences in age. However, the Mean Increments show that the rates of stipe elongation and pneumatocyst enlargement were much higher than those for mature plants in the plots. The average rate of stipe elongation for these transect plants was about 6 cm per month. The transect plants were not followed long enough to determine maximum age, but within about four months from the time of labelling, approximately 50% of the sample remained.

Measurements of Light and Temperature

Light measurements were made with a single underwater unit consisting of a Weston self-generating barrier layer cell (Type 856RR) mounted in a water-tight housing.[2] The barrier layer cell was shielded from the water by a braded translucent plastic collector with cosine collecting properties. A Wratten 45 blue-green filter (440-530 mμ, peak at 490 mμ) was used in the underwater unit with one to several Kodak neutral density filters. The barrier layer cell was connected to a 100 microamp meter contained in a transparent plastic housing by water-tight rub-

[2] Construction of light apparatus was based on a design used by Robert L. Holmes, Scripps Institution of Oceanography, La Jolla, California.

Table 2. Measurements of Stipe Elongation and Pneumatocyst Width Expansion of *P. giganteus* Young Plants in Plots 1 and 2 and Transect.

	DATES ⟶ NO. PLT.	10-11-64	11-28-64	1-16-65	2-1-65	2-13-65	3-20-65	4-24-65	6-16-65
PLOT 1	A02	22 (1.93)	Gone						
PLOT 2	A01	47 (4.45)	73 (5.72)	—	—	92 (6.35)	Gone		
	A03	43 (3.81)	61 (4.78)	62 (4.78)	—	65 (5.08)	Gone		
	A04	44 (4.11)	Gone						
	A05	43 (3.81)	78 (4.78)	95 (4.78)	96 (5.08)	Gone			
	A06	87 (5.38)	136 (6.65)	163 (7.32)	163 (7.32)	161 (7.62)	166 (7.92)	183 —	202 (9.19)
	A07	82 (5.38)	130 (6.35)	140 (6.99)	140 (6.99)	150 (6.99)	155 (7.62)	169 —	192 (8.89)
MEAN INCREMENTS			33.2 (1.15)	13.8 (0.33)	0.33 (0.10)	7.5 (0.31)	5.0 (0.46)	15.5 —	21.0 (1.27)
LINE TRANSECT	D1				157 (5.08)	157 (5.08)	160 (5.38)	170 (5.72)	Gone
	D3				49 (3.48)	48 (3.81)	46 (3.81)	50 (3.81)	Gone
	D4				135 (6.65)	137 (6.35)	148 (6.65)	148 (6.99)	155 (7.62)
	D5				108 (5.08)	111 (5.38)	120 (6.02)	125 (6.35)	138 (7.32)
	D6				266 (5.08)	269 (5.38)	279 (7.32)	— —	314 (7.92)
	D7				211 (7.92)	212 (7.80)	— —	225 (8.57)	229 (9.19)
	D8				195 (—)	Gone			
	D9				192 (6.02)	193 (5.72)	193 (6.02)	204 (6.35)	224 (6.99)
	D10				54 (3.81)	53 (4.45)	56 (4.78)	62 (5.08)	72 (5.72)
	D11				222 (5.72)	223 (6.02)	226 (5.10)	— —	252 (7.32)
	D12				30 (3.18)	32 (2.72)	Gone		
	D13				165 (6.35)	177 (6.99)	191 (7.62)	197 (8.25)	205 (8.57)
	D16				168 (5.72)	— —	191 (6.65)	192 (5.72)	Gone
	D17				30 (3.18)	31 (2.72)	Gone		
	D18				26 (2.84)	28 (2.84)	Gone		
	D19				231 (8.25)	— —	264 (8.25)	286 (8.25)	Gone
	D20				135 (6.99)	Gone			
	D21				33 (3.81)	33 (4.11)	33 (4.11)	35 (4.22)	35 (4.45)
	D23				48 (3.81)	50 (3.48)	49 (3.48)	Gone	
	D25				110 (6.35)	115 (6.35)	120 (6.99)	125 (7.62)	Gone
MEAN INCREMENTS						1.75 (0.06)	5.57 (0.37)	7.73 (0.15)	13.6 (0.69)

Table 3. Surface and bottom temperatures recorded with bathythermograph at Long Point.

Date	Temperature, C° Surface	25 Meters	Date	Temperature, C° Surface	25 Meters
2-1-64	14.7	14.7	10-11-64	19.4	16.5
2-8-64	14.4	14.4	11-28-64	14.9	14.2
3-28-64	14.4	14.4	11-29-64	14.9	14.5
5-2-64	14.7	14.4	12-20-64	13.3	13.0
6-10-64	17.2	12.0	1-16-65	12.5	12.4
7-9-64	18.1	16.2	1-17-65	13.5	13.2
7-10-64	18.0	11.4	2-1-65	13.5	13.5
7-11-64	18.5	15.0	2-2-65	13.5	13.0
7-12-64	18.5	11.9	2-13-65	13.5	13.0
7-25-64	20.1	13.9	2-14-65	13.3	13.0
7-26-64	19.5	12.9	4-24-65	15.3	15.0
8-1-64	21.5	14.0	6-15-65:		
8-2-64	21.2	13.5	8:00am	16.2	14.0
9-12-64	19.9	16.9	12:00	16.0	14.0
10-10-64	20.0	17.2	4:30pm	15.8	13.5
			8:00pm	15.8	12.5

ber wire couplings. For underwater measurements, the equipment was carried by diver to the plots and read directly at the level of *P. giganteus* blades (ca 80 ft depth). Prior to each set of bottom measurements, a cap containing one or more additional neutral density filters was placed over the photo-cell housing and a reading of the surface blue-green illumination was made. Subsequently, all filters and filter combinations were calibrated in full sunlight at the authors' laboratory using a thermopile as described by Bulpitt *et al.* (1965).

The underwater apparatus was completed in November, 1964. Therefore, our data is not complete for the year-round study and our results must be limited to a few brief statements.

Considerable variation occurs in the percentage of surface blue-green illumination penetrating to the depth of our experimental plots. On January 17, 1965, as little as 2.6% of the surface midday blue-green illumination penetrated to the plots. This constituted approximately 2382 ergs sec^{-1} cm^{-2}. Our highest reading was recorded March 20, 1965, at 11.45 am, when about 24% of the surface blue-green illumination (ca 23,000 ergs sec^{-1} cm^{-2}) reached the blades of the tagged plants. The average of our monthly, midday, bottom readings between November, 1964, and June, 1965, is approximately 8% of the surface blue-green illumination. The illumination beneath blades of *Pelagophycus* was consistently too small to be detected by our equipment.

On February 2, 1965, a deep dive was made to the outer periphery of the *P. giganteus* population at Long Point. The population extended to about 125 ft depth where the irradiance constituted 0.7% of the surface blue-green illumination.

A bathythermograph was used for temperature measurements from surface to depth of the experimental plots. The surface and bottom temperatures are recorded in Table 3. From February 1 to May 2, 1964, the surface and bottom temperatures were approximately the same (ca 14.5 C). This same condition prevailed between November 28, 1964 and April 24, 1965. However, the period from June to October,

1964, included higher surface temperatures than bottom temperatures. This summer period was characterized also by a thermocline (i.e. mixed layer), the depth of which changed hourly and daily. On occasions the thermocline reached 75 ft depth, creating drastically different temperatures for the blades and pneumatocysts of plants which extended into the epilimnion and the stipes and holdfasts located in the hypolimnion. However, generally the thermocline occurred at or above 55 ft depth at Long Point which lay above most of the population of *P. giganteus*.

Transplanting of P. porra Juvenile Sporophytes to Long Point

Preliminary to the transplanting experiment, a mature *P. giganteus* specimen was detached from the substratum and pulled to the surface. After 24 hr at the surface, this plant was returned to the bottom at about 80 ft where the holdfast was covered with the silty-sandy substratum. This plant remained several months intact and exhibited no damage to pneumatocyst or other parts. On the success of this venture, 105 juvenile *P. porra* sporophytes were collected from depths of 40-75 ft off La Jolla, California. The smallest specimens had no pneumatocysts, while the largest ones had pneumatocysts up to 6 cm in maximum width, all being spherical. Except for six of the plants which had four blades, all others had one or two blades. All plants were stored nearly 48 hr in circulating seawater tanks at Scripps Institution of Oceanography, then placed into wet burlap sacks and transported 125 mi to San Pedro, California. The sacks were immersed in the sea overnight, and then taken by boat to Long Point. Thus 72-96 hr following collection, the 105 juvenile *P. porra* specimens were replanted. Near the two experimental plots of *P. giganteus*, a 50 ft nylon line was stretched out and secured by aluminum stakes. Large native seaweeds were removed from an area 3 ft to either side of this line. The juvenile *P. porra* plants were then planted along the line at approximately 3 ft intervals. At least 20 of the transplants were still attached to their rocks, as is characteristic of the species; these needed no further attachment. The remaining unattached specimens were fastened to the sandy-silty substratum by two large wire pins, each bent in the shape of a hair pin and inserted through the holdfast at opposing angles with the two prongs anchored in the substratum. Each specimen had a small plastic tag secured to it prior to planting. The transplanting was accomplished on December 19-20, 1964, during very rough weather with some bottom turbulence.

The day after the transplanting, a brief visit to the site revealed that approximately 10 specimens with the smaller holdfasts had been lost during the bottom turbulence. An additional 20 or so plants with 3-6 cm pneumatocysts lay on the bottom, their pneumatocysts collapsed and broken.

The site was next visited on January 16, 1965. Only two of the transplanted *P. porra* sporophytes had survived intact. These two had been among the smallest specimens and lacked well-developed pneumatocysts. Measurement showed that none of the organs had grown during the four weeks at Long Point. The remaining plants had imploded pneumatocysts and/or lacked intact blades. Their holdfasts, stipes, and antlers were intact.

Laboratory Cultivation of Zoospores and Gametophytes of P. giganteus

Pieces of sporophylls of *P. giganteus* were brought to the laboratory on February 2, 1964. Following 48 hr storage at ca 5 C in a refrigerator, square centimeter pieces of sori were cut, washed in sterile seawater, and placed in Petri dishes containing autoclave-sterilized enriched seawater medium (Parker, 1965). Cultures were maintained at 10 C under 50-200 ft-c constant illumination from cool-white fluorescent lamps. Microscopic observations of the contents of dishes were made daily.

Twenty-four hr after immersion of soral pieces into the medium, cultures were teeming with biflagellate zoospores, each 4 × 5 μ. About 32 zoospores continued their emergence from certain unilocular zoosporangia. Zoospores were typically reniform with laterally inserted flagella, one projecting anteriorly and the other posteriorly when swimming unidirectionally (Fig. 6). Soral pieces were removed after 48 hr and aliquots of culture liquid containing spores were transferred to fresh, sterile media, and subsequently maintained at 14.5 C (the measured temperature of the natural environment of *P. giganteus* at Long Point). This was considered zero time.

Two days later, motility of zoospores had ceased and spherical cells with rigid walls and several plastids were abundant on the bottom of Petri dishes. Cultures eight days old still contained many single cells, most of which had enlarged to 6 μ or more. By 18 days, 2-, 3-, and 4-celled germlings were common (Fig. 7), and by the end of 28 days, 8- to 12-celled germlings had developed. At this point, a number of larger germlings (12 or more cells) were transferred to fresh media. Forty days after inoculation of zoospores, these germlings had become multibranched filaments of more than 100 cells. The cells of some germlings appeared smaller than those of others within the same culture, calling to mind the distinction into micro- and megagametophyte made by Herbst & Johnstone (1937) in their study of the *P. porra* life cycle. A few of the larger-celled germlings possessed enlarged terminal cells resembling oogonia of *P. porra.* The fate of these enlarged cells was not ascertained, and cultures were again transferred. By the end of 60 days, presumed sporophytes consisting of short uni- and multiseriate filaments of cells appeared in cultures. These were both free-floating and attached to the germlings which had smaller cells (Fig. 8). Following another transfer into fresh media and by 90 days (May 2, 1964), a few presumed sporophytes had developed monostromatic blades of several hundred cells with rhizoids at the base (Fig. 9). Further development of sporophytes within our cultures could not be induced although a variety of methods were tried including shaking the flasks and planting in sterile sand or soil.

Discussion

Our studies of *Pelagophycus giganteus* at Long Point for approximately 1½ years have indicated that a seasonal regulation of the life-cycle of this giant benthic seaweed takes place. This conclusion is supported by a sequence of observations, as follows: (1) Only adult plants constituted the population between the late fall of 1963 and May, 1964; (2) Sporophylls first appeared in February, 1964; (3) A spon-

Fig. 5. Upper portion of *P. giganteus* at ca 90 ft depth at Long Point, showing upper stipe and pneumatocyst, antlers, and six blades in their typical drooping habit; ca ×0.1. Fig. 6. Biflagellate zoospore of *P. giganteus*; ×1800. Fig. 7. Two-celled gametophyte, 18 days after release of zoospores; ca ×1800. Fig. 8. 60-day-old gametophytes in culture with predominantly uniseriate sporophytes (larger cells); ×425. Fig. 9. Two monostromatic sporophyte blades of *P. giganteus* attached to female gametophytes after 90 days of culture; ×100.

taneous appearance of tiny sporophytes occurred in May, 1964; (4) Our cultures of zoospores developed into microscopic germlings resembling gametophytes of other *Laminariales* (Fritsch, 1945), and produced macroscopic sporophytes within 90 days, a length of time which coincided with the first appearance of sporophytes in the natural environment. *Nereocystis luetkeana,* a close relative of *Pelagophycus,* also has a seasonal production of sporophylls and juvenile sporophyte plants (Frye, 1906; Rigg, 1917; Setchell, 1908; McLean, 1962).

We have no reasons from our observations of unilocular sporangia, zoospores, germlings, and young sporophytes to suppose that *P. giganteus* has not a normal sexual life-cycle representing heteromorphic alternation of diploid sporophytic and haploid gametophytic generations. Our observations of morphology and the sequence of events resemble closely the life-cycles of *Macrocystis* and *Nereocystis* (Scagel, 1947) as well as that of *Pelagophycus porra* (Herbst & Johnstone, 1937). The germlings are quite likely gametophytes although this conclusion is not irrefutable without further observations of meiosis and gametogenesis.

Numerous factors doubtless play a role in regulating the production of sporophylls, release of zoospores, development of gametophytes, gametogenesis, fertilization, and subsequent development of the young sporophyte generation, but the most influential factor suggested by our studies was temperature. The lowering of the water temperature to 15 C or less appears to have triggered the differentiation of sporophylls and subsequent phenomena which occurred during the winter and spring of 1964. Long Point water temperatures during the late spring and summer of 1964 were abnormally cool compared with previous unpublished reports for the several preceding years. Consequently sporophylls continued their production of spores throughout the summer until September when the water temperature at the level of *P. giganteus* finally rose above 15 C. The temperature of 14.5 C in both natural environment and our laboratory cultures was suitable for development of germlings and at least a limited number of very young sporophytes. These temperatures are somewhat above those (8-12 C) shown to be optimal for germling (also assumed to be gametophyte) development in *P. porra* from the cooler coastal waters near San Pedro, California (Herbst & Johnstone, 1937).

It is noteworthy that several earlier workers arrived at a similar temperature-regulated life-cycle theory for other *Laminariales.* Schreiber (1930) found that lowering the water temperature to 4-6 C induced gametogenesis, whereas raising the temperature to 18 C suppressed this process in *Laminaria.* Hartge (1928) cultured *Nereocystis* at 16 C. Myers (1925, 1928) and McKay (1933) considered 12-16 C optimal for growth and reproduction of *Nereocystis,* and noted that gametophytes developed at 4 C but failed to produce gametes at 12-20 C. Fritsch (1945) further substantiates that the development of sori ". . . usually coincides with the cold season, and the fertile parts often persist through a considerable part of the winter."

Our data have revealed that a high mortality occurs among juvenile *P. giganteus* sporophytes in the natural environment, and that those plants which do survive to a reproductive stage generally do not live beyond that year. This demonstrates that *P. giganteus* is, for the most part, an annual plant. A few individuals tagged in

our study, which had mature, reproductive sporophylls initially, lived for more than a year. These plants in Plots 1 and 2 were apparently at least 6 months old when first tagged, so it is possible that some individuals survive two reproductive seasons and a few may reach two years of age.

Pelagophycus porra and *Nereocystis luetkeana* are also annual plants (Setchell, 1912), while *Macrocystis* is generally considered a perennial (Scagel, 1947), its individual fronds being of a seasonal or annual nature (North, 1961).

Our data on stipe elongation and pneumatocyst enlargement, indicate that the plants first tagged in Plots 1 and 2 were fully grown and subsequently grew at relatively slow rates. In contrast, the younger individuals tagged grew at rates 6-10 times as fast as the mature plants. Unfortunately the delicate construction of very small juveniles and the relatively clumsy techniques which are an inevitable accompaniment to scuba diving prevented our obtaining data on the growth rates of very young sporophytes within the Long Point population.

Our light measurements are only approximations but suggest that 5-10% of the blue-green illumination at the surface penetrates to the depth of 80 ft near the center of the population of *P. giganteus*. This population continues further to 125 ft depth where the blue-green light is reduced to less than 1% of that at the surface. It must be realized that these approximate percentages represent blue-green light only. It is, therefore, meaningless to compare our data with that from laboratory studies. For example, Neushul & Haxo (1963) found that sporophytes of *Macrocystis* required a minimum of approximately 600 lux of continuous, fluorescent light to develop. Our data do not permit us to calculate the total downwelling irradiance, nor to equate this spectral diurnal illumination at 125 ft with the full spectrum of constant illumination used by these workers. Further examination of the light energy reaching *Pelagophycus giganteus* in nature and in laboratory will, no doubt, help define its limits more precisely.

Of interest in connection with adaptation of *Pelagophycus* to low light requirements is an observation we first made while collecting specimens of *P. giganteus* at San Clemente Island during 1963. Plants taken from a depth of 125 ft were chocolate in color, while plants collected at 90 ft or less were lighter brown, presumably due to differences in concentration of fucoxanthin. All plants were approximately the same size with approximately equal total blade surface areas. Obviously the ability of seaweeds to tolerate smaller amounts of light energy also may relate to the total area of photosynthetic surface per individual plant. We note, therefore, that McLean (1962) reported the typical *Nereocystis luetkeana* adult possessed a total blade surface area of 70 sq ft; mature *Nereocystis* blades usually float at the surface. In comparison, *P. giganteus* adults typically possess about 360 sq ft of total blade surface at a depth of 70 ft (data from Parker & Dawson, 1964). A more exhaustive study of photo-synthetic surface area for a variety of marine algae at different depths has not, to our knowledge, been made.

The attempted transplanting of *P. porra* from its coastal habitat to the Long Point habitat of *P. giganteus* was for the most part unsuccessful, yielding little information. No doubt many of the transplants died as a result of imploded pneumatocysts. This probably was caused by a reduced pressure of gases in the

pneumatocysts when the plants were collected and maintained at the surface for 72 or more hours before being returned to a depth of 80 ft or more. Neushul & Haxo (1963) encountered similar difficulties in their transplanting attempts with *Macrocystis.* However, a number of ours smaller plants lacked well-developed pneumatocysts and therefore could not have failed to grow because of injury to this organ. Neither was there any clear indication of excessive grazing of the *P. porra* plants by animals. Two plants whose blades remained intact for four weeks showed no signs of growth in either stipe length or pneumatocyst diameter. This suggests that had the other plants remained intact, they too probably would not have grown. We, therefore, draw the tentative conclusion that *P. porra* cannot develop in the environment of *P. giganteus,* and our evidence thus confirms that these are two distinct species, and not merely ecophenes.

If the germlings which developed from the zoospores were gametophytes, as we suspect, then *P. giganteus* has the kind of heteromorphic alternation of generations which is typical of other members of the *Laminariales.* The spores released were biflagellate and actively motile, in contrast to those of *P. porra* which, accord- to Herbst & Johnstone (1937), were non-flagellated. Also, the zoospores of *P. giganteus* were $4 \times 5\ \mu$, while those of *P. porra* were $3.5 \times 4.0\ \mu$ in diameter. This difference in size, although seemingly small, constitutes a two-fold difference in the calculated volumes of these respective spores; the zoospores of *P. giganteus* are approximately twice the volume of spores of *P. porra.* This suggests to us that the nuclear volumes of these species may also be different by a factor of 2. This has already been reported by Parker & Fu (1965) who found that the nuclear volumes of *P. giganteus* meristoderm cells were precisely twice that of *P. porra* meristoderm cells. They concluded that *P. giganteus* might be a polyploid species derived from *P. porra.* Our observations of germling development and sporophyte production are, primarily, like those reported by Herbst & Johnstone (1937) for *P. porra,* and hence, require no further discussion here.

These investigations have contributed to our understanding of the ecology of *Pelagophycus.* They have answered a number of important questions about this genus and have pointed the way to further areas of fruitful investigation of benthic seaweeds using the scuba diving technique.

Literature Cited

Bulpitt, T. H., M. W. Coulter, & K. C. Hammer. 1965. A spectroradiometer for the spectral region of biological photosensitivity. Appl. Op. **4**: 793-797.

Dawson, E. Y. 1962. On the recognition of a second species of the genus *Pelagophycus.* Bull. So. Calif. Acad. Sci. **61**: 153-160.

Fritsch, F. E. 1945. The structure and reproduction of the algae. Vol. 2, 1-939. Cambridge Univ. Press.

Frye, T. C. 1906. *Nereocystis luetkeana.* Bot. Gaz. **42**: 143-146.

Hartge, L. A. 1928. Nereocystis. Publ. Puget Sound Biol. Sta. **6**: 207-237.

Herbst, C. C. & G. R. Johnstone. 1937. Life history of *Pelagophycus porra.* Bot. Gaz. **99**: 339-354.

McKay, H. H. 1933. Life history of *Pterygophora californica.* Univ. Calif. Publ. Bot. **17**: 111-148.

McLean, J. H. 1962. Sublittoral ecology of kelp beds of the open coast area near Carmel, California. Biol. Bull. **122**: 95-114.

Myers, M. E. 1925. Contributions towards a knowledge of the life-histories of the *Melanophyceae*. A preliminary report. Univ. Calif. Publ. Bot. **13**: 109-124.

———. 1928. Life-history of the brown alga, *Egregia menziesii*. Univ. Calif. Publ. Bot. **14**: 225-246.

Neushul, M. & F. T. Haxo. 1963. Studies on the giant kelp, *Macrocystis*. I. Growth of young plants. Amer. Jour. Bot. **50**: 349-353.

North, W. J. 1961. Life-span of the fronds of the giant kelp, *Macrocystis pyrifera*. Nature **190**: 1214-1215.

Parker, B. C. 1965. Translocation in the giant kelp *Macrocystis*. I. Rates, direction, quantity of C^{14}-labelled products and fluorescein. Jour. Phycol. **1**: 41-46.

———, & J. Bleck. 1965. A new species of elk kelp. Trans. San Diego Soc. Nat. Hist. **14**: 57-64.

———, & E. Y. Dawson. 1964. Notes on variability and range in the elk kelp *Pelagophycus*. Trans. San Diego Soc. Nat. Hist. **13**: 303-307.

———. 1965. Non-calcareous marine algae from California miocene deposits. Nova Hed. X(1 + 2): 273-295, *pl. 76(1)-96(21)*.

———, & M. Fu. 1965. The internal structure of the elk kelp (*Pelagophycus* species). Canad. Jour. Bot. **43**: 1293-1306.

Rigg, G. B. 1917. Seasonal development of bladder kelp. Publ. Puget Sound Biol. Sta. **1**: 308-318.

Scagel, R. F. 1947. An investigation on marine plants near Hardy Bay, B.C. Prov. Dept. Fish., Victoria, B.C., No. 1: 1-70.

Schreiber, E. 1930. Untersuchungen über parthenogenesis, geschlechtsbestimmung und bartardierungsvermögen bei Laminarien. Planta **12**: 331-353.

Setchell, W. A. 1908. *Nereocystis* and *Pelagophycus*. Bot. Gaz. **45**: 125-134.

A PRELIMINARY ULTRASTRUCTURAL STUDY OF THE FRESHWATER RED ALGA COMPSOPOGON

BY H. WAYNE NICHOLS, JOHN E. RIDGWAY AND HAROLD C. BOLD

Department of Botany, Washington University, St. Louis, Missouri and
Department of Botany, University of Texas, Austin

ABSTRACT

Certain aspects of cellular organization of *Compsopogon coeruleus* have been studied by light and electron microscopy. Chloroplasts arise from proplastids or by constrictions (equal or unequal) of mature plastids. A lamellar reorganization is evident during plastid division. The chloroplasts are not parietal sheets as previously thought from light-microscopic observations but, instead, are closely associated discs. Furthermore, the discs are not connected but appear to be so because of their close association with cytoplasmic and vacuolar membranes. Floridean starch has been observed to be associated with cytoplasmic membranes and the nucleus but is seldom in close association with the chloroplasts. There are no 'true' pits between cells, but a continuation of adjacent protoplasts occurs when the cells are undergoing rapid karyokinesis without completion of cytokinesis. Organelles which are similar to those reported in other algae and angiosperms are briefly described.

Several problems concerning the developmental morphology of the red alga *Compsopogon coeruleus* arose after prolonged studies of the alga in culture (Nichols, 1964). These problems primarily concern the origin and development of chloroplasts and the morphological nature of cell walls of this plant. Preliminary studies have been directed to these and related problems.

The chloroplasts of *Compsopogon coeruleus* previous to this paper were thought to undergo characteristic changes during cellular ontogeny from parietal sheets, in uniseriate filaments and spores, to discoid chloroplasts, which occur in bands, and which apparently remain connected by cytoplasmic strands in older cells (Nichols, 1964). Chloroplast development in this alga poses several fundamental questions: (1) Do the chloroplasts arise from proplastids? (2) Do the disc-like forms arise from segmentation of the parietal sheet-like chloroplast in spores and uniseriate filaments? (3) When a chloroplast divides, what are the lamellar changes, if any? (4) What is the nature of the connecting strands between discoid plastids in older cells? These questions are significant, since the chloroplasts of many photosynthetic cells have been found to contain or be associated with quantities of genetic material, nucleic acids, (Sager, 1962; Ris & Plaut, 1962; Sager & Ishida, 1963).[2]

Cell wall studies of *Compsopogon* are important to us since the genus is classified as a member of the *Bangiophycidae* (Papenfuss, 1955). Plants in this sub-

---

[1]This study was supported in part by a grant from the National Science Foundation (NSF GB 313) to Harold C. Bold and W. G. Whaley and grants from the American Cancer Society (ACS IN-36E) and the National Science Foundation (NSF GB 4377) to H. Wayne Nichols.

[2]Nucleic acid determinations of isolated chloroplasts of *Compsopogon* are presently being made in addition to a continuation of present studies related to chloroplast and cell wall development.

class are regarded by most phycologists as lacking pit connections. However, pits have been reported in *Compsopogon* (Fan, 1960). These connections and their taxanomic significance have been discussed recently (Dixon, 1963). Dixon has suggested a need for ultrastructural studies of this plant and other bangiophycean genera to verify the occurrence of 'true' pit connections.

Materials and Methods—Plants derived from single monospores of *Compsopogon coeruleus* (Balbis) Mont. were grown under standard laboratory conditions (21 C, 12/12-hr. light-dark cycle, 250 ft-C florescent illumination). The plants were maintained in a liquid medium (Bischoff & Bold, 1964) or agarized (1.5%) with physical modifications as follows. Agarized medium was added to large Petri dishes and slanted, thus leaving a side of the culture vessel free from the solidified medium. This reservoir was then filled with the liquid medium and single spores inoculated on the slanted agar surface.

The cultured material was fixed either in a 2% aqueous solution of unbuffered $KMNO_4$ at 4 C for 1½ hr (Mollenhauer, 1959), or in a 2% OsO_4 solution buffered to pH 7.4 with 0.2 M sodium cacodylate (Plumel, 1948) at 4 C for 1½ hr. After washing with cold distilled water, the material was dehydrated in a graded ethanol series of 25%, 50%, 70,% 95,% and 2 changes of 100%, each step lasting a minimum of 10 min. The material was then passed through 2 changes of 100% acetone and embedded in a graded series of mixtures of the epoxy resin araldite 506 (Ciba Products Corporation, Fair Lawn, N.J.) and Epon Resin 812 (Ring Chemical Company, Houston, Texas (Mollenhauer, 1964). Small blocks containing the material were cut from plastic and glued to dowels for proper orientation. Sections showing a silver interference color were cut with a diamond knife on a Porter Blum ultramicrotome. They were then picked up on copper mesh grids post-stained with lead hydroxide (Millonig, 1961) for 20 min. All sections were examined with an RCA EMU 3D electron microscope.

Observations—*Compsopogon coeruleus* is a filamentous member of the *Bangiophycidae.* The uniseriate filaments become corticated at maturity by periclinal divisions of the older cells. Growth is primarily apical, but intercalary divisions do occur when the filaments are growing rapidly and when uniseriate filaments are becoming corticated. Young uncorticated filaments, as well as older corticated ones may comprise a single plant with additional cortical development as the filaments age. Reproduction in *Compsopogon* is effected asexually by monospores produced from filaments of varying ages, or by fragmentation of the plant body.

Vacuoles are difficult to distinguish in the alga but appear to be centrally located (Fig. A,B). There is a single, large vacuole in each cell. The ellipsoidal nucleus is usually central, but the position is variable.

The chloroplasts of *Compsopogon coeruleus* are parietal, closely associated discs during early stages of development (Fig. A-D, 1,4). This association is gradually terminated as the cells enlarge. When mature, the cells are larger and the chloroplasts are distributed throughout the cytoplasm (Fig. E-F).

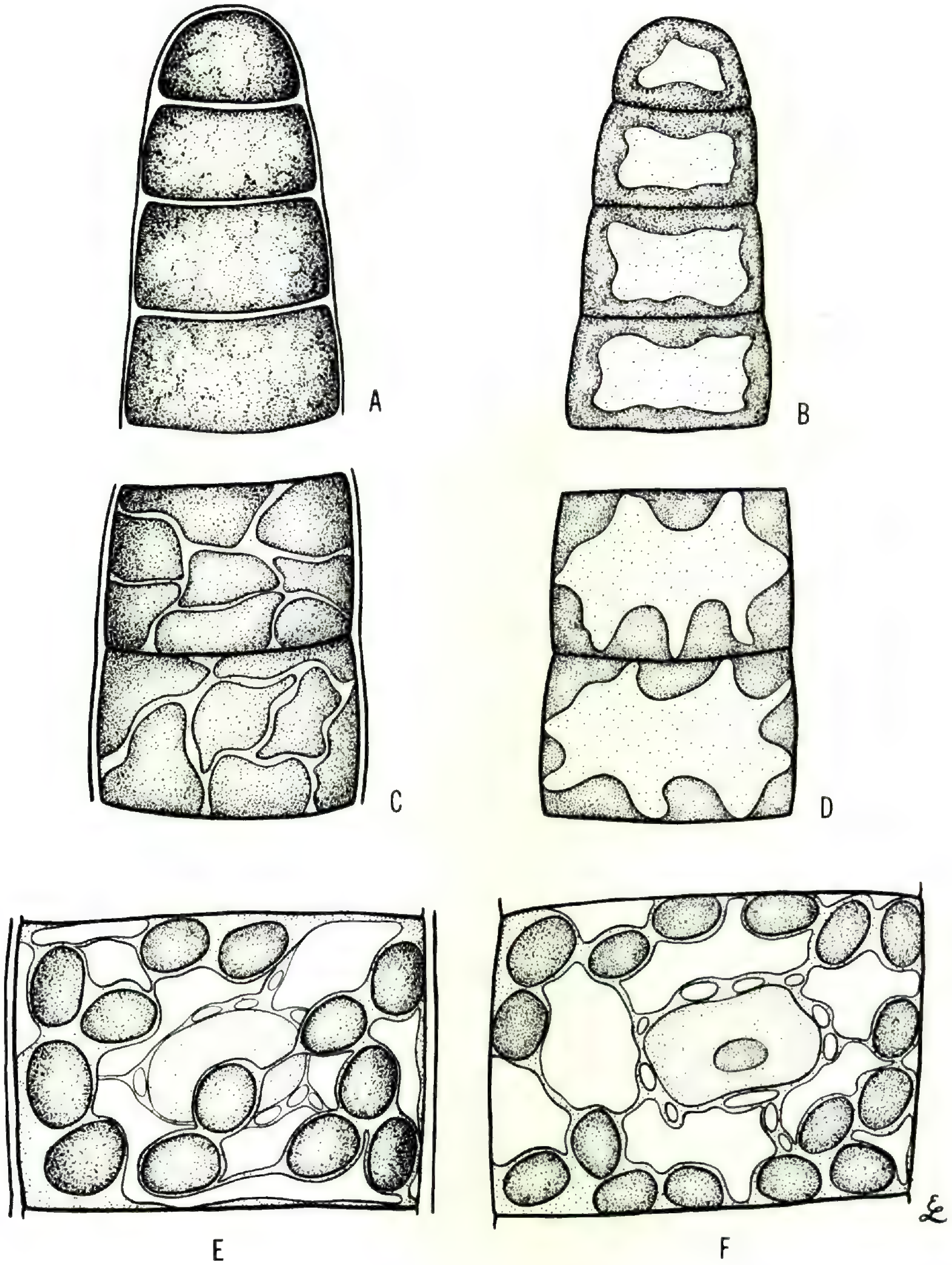


Fig. A-F. *Compsopogon coeruleus.* Fig. A-B. Surface and median longitudinal section of uniseriate filament apex. Fig. C-D. Surface and median longitudinal section of older cells in a uniseriate filament. Fig. E-F. Surface view and median longitudinal section of mature cells of a uniseriate filament. All drawings were made from living material and are diagramatic.

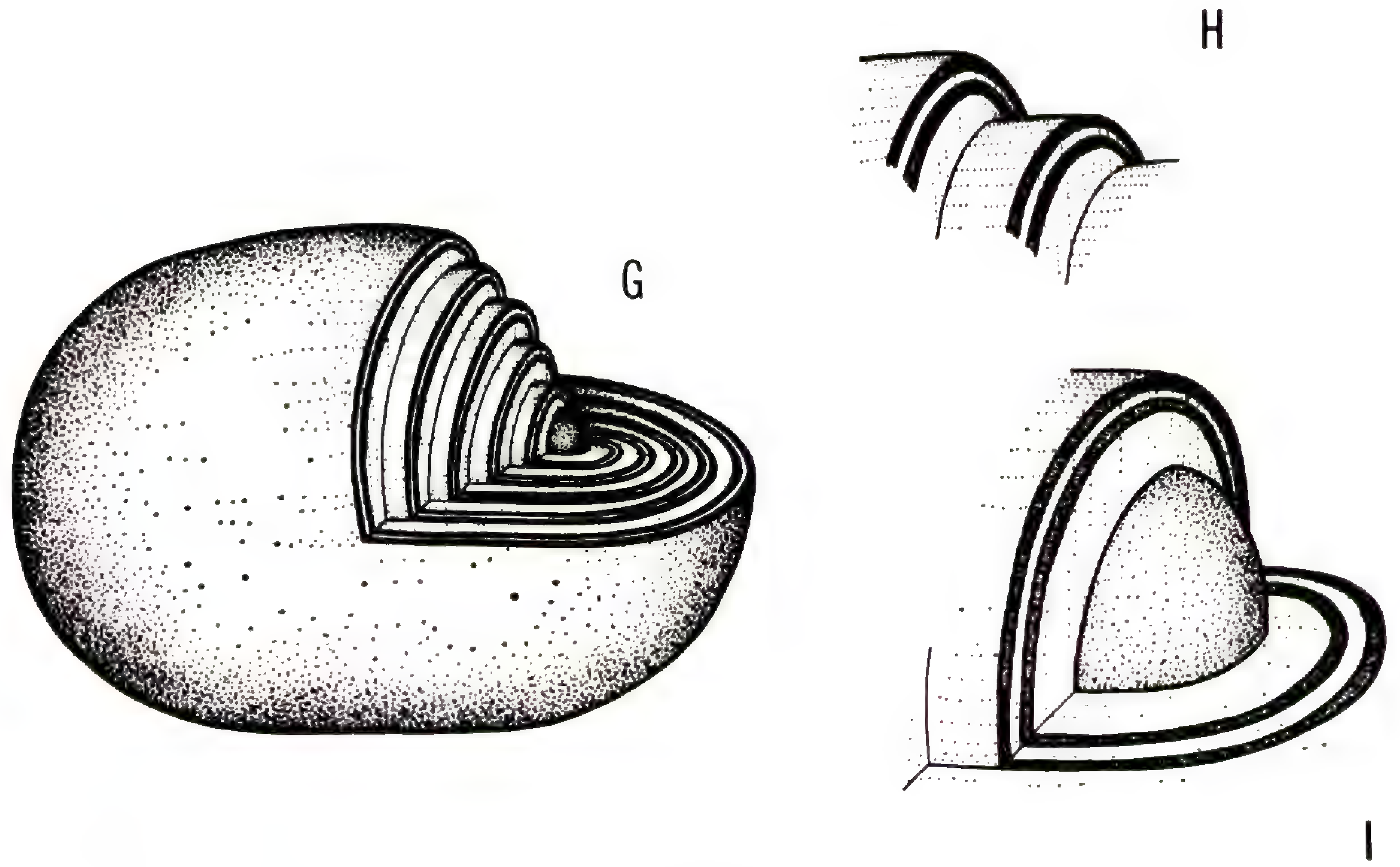


Fig. G-I. *Compsopogon coeruleus.* Fig. G. Reconstruction of a chloroplast from light and electron micrographs. Fig. H-I. Detail of lamellar structures in a single chloroplast.

Each chloroplast is bounded by two limiting membrances (Fig. 5). Internal to these are concentrically arranged, equidistant lamellae which traverse the matrix (Fig. 3,4). The lamellae are apparently sheet-like flattened sacs for when the chloroplasts are sectioned obliquely, the lamellae appear as solid, electron-dense sheets within the boundary of the outer limiting membranes (Fig. G-I, 15).

The chloroplasts of *Compsopogon* arise in at least two (different) ways. They may arise from proplastids which are particulate fractions within the cytoplasm.[3] The proplastids are distinguishable from mitochondria by their outer limiting membrane, closely associated inner membrane and a complete absence of lamellar structure. However, in later development, lamellae are formed which bisect the proplastid (Fig. 11,12). The mechanism of further development of lamellae is at present unknown, but the outcome of development is the formation of concentric rings of lamellae within the outer limiting membranes.

Chloroplasts may also arise by an apparently more complex series of events which involve the mature, well-developed plastids. These chloroplasts undergo gradual constrictions. The constrictions may be median or marginal (Fig. 6,10,12, 16). In some instances, the constriction resulted in segments of the chloroplasts being cut off which were morphologically similar to proplastids (Fig. 12,16). Dur-

[3] See Bouck (1962), Weier (1963), and Ben-Shaul, Schiff & Epstein (1964) for discussions concerning controversies and problematical observations on the ontogeny of particulate bodies (proplastids) of photosynthetic cells. We refer to proplastids throughout this paper as double-membraned organelles, similar morphologically and ontogenetically to those described by Ben-Shaul, Schiff, & Epstein (1964) in *Euglena gracillis* var. *bacillaris* Pringsheim.

ing median or marginal constriction, the lamellae undergo characteristic reorganization. The outer limiting membranes indent centripetally coincident with the indention of the first lamellar ring (Fig. 7-8). The outer limiting membranes usually remain intact until completion of division, while the lamellar rings break and become reorganized (Fig. 9-10). Whether the outer limiting membranes break and fusion of terminal portions occurs is unknown. Division may occur simultaneously in more than two areas of the same chloroplast and result in the formation of several plastids derived from a single chloroplast.

The chloroplasts, when mature, may be associated with other cellular constituents. The most obvious association is between chloroplasts and cytoplasmic strands. These strands lie close to the plastid and appear to ensheath it (Fig. 2). However, we have found no intimate connections between these membranes and chloroplasts. The vacuolar membranes often extend into the nuclear area (Fig. 17, F). These membranes traverse the cell and form a network throughout the vacuole. Chloroplasts may extend into the nuclear area and become bounded by the vacuolar membranes (Fig. 15, 16). These membranes are single, although adjacent ones often occur in close proximity if chloroplasts or floridean starch grains do not separate them.

A second relationship within the cells of *Compsopogon* is also apparent. This involves the prominent strands in the cytoplasm. Here, it is easy to distinguish the associated floridean starch grains. These elongate grains accumulate around the nucleus and between the cytoplasmic strands which traverse the vacuole and terminate in the nuclear area (Fig. 13,21,F). This product is seldom in close proximity to the chloroplasts.

The cell walls of this alga are deposited centripetally (Fig. 14, 22). When young they consist of at least two differentiated layers (Fig. 23, 25). However, with age, the cell walls become multilayered (Fig. 20). No pit connection similar to those commonly found in floridean algae have been observed in *Compsopogon* (Fig. 23, 24). Cytoplasmic connections have been observed between cells in which there was an incomplete deposition of wall material. Here the cytoplasm is continuous and typical organelles, including chloroplasts, have been observed.

Other organelles were observed. The Golgi bodies are typical, vesiculate structures similar to those reported in other plants. The mitochondria are circular in cross section with an outer and inner membrane. In longitudinal section, they are elliptical. The inner membrane exhibits numerous changes from circular invaginations to connections between cristae from opposite sides of the mitochondrion (Fig. 18, 19). Some inner membrane invaginations give rise to typical cristae, while the inner membrane in most instances is variable.

Discussion—It is clear from the past discussions and observations of Ueda (1962) and Weier (1963) that chloroplasts in various algal and angiosperm groups are variable. In *Compsopogon*, a so-called primitive red alga, we have encountered developmental stages which are similar to those reported for algae in different taxonomic groups. For example, concentric lamellar structures like those described by Weier (1963) in *Nostoc*, a blue-green alga, are present; median constriction of dividing chloroplasts in *Compsopogon* is apparently similar to that

in the red alga *Lomentaria* (Bouck, 1962). The latter is considered by many systematists to be a more 'advanced' red alga and is taxonomically in a different subclass, the *Floridiophycidae*. Thus, we may conclude that morphological characteristics which are considered primitive or advanced by many investigators are not necessarily reflected at the ultra-structural level.

Cell walls of *Compsopogon* are without pit connections. The former are deposited centripetally after karyokinetic divisions. However, there may be incompletely deposited walls when karyokinesis is rapid. These openings are not pits but contain typical cellular organelles within the cytoplasm. Pit structures similar to those reported by Myers, Preston & Ripley (1959), Bouck (1960), and Bischoff (1964) have not been observed in *Compsopogon*.

The morphology of mitochondria and Golgi bodies in *Compsopogon* is not strikingly different from that of *Porphyridium* (Brady & Vatter, 1959), *Lomentaria* (Bouck, 1962), *Thorea* (Bischoff, 1964) or even angiosperms (Esau, 1963).

Finally, we have demonstrated that a chloroplast type is present in *Compsopogon*, a red alga, which is morphologically similar to photosynthetic apparati observed in some cyanophycean genera. We have confirmed or clarified previously published light microscope observations as follows:

(A) Cell walls are deposited centripetally.

(B) No pit connections are present in *Compsopogon*.

(C) Chloroplasts are not sheet-like in young cells but closely associated discs.

(D) Chloroplasts are not connected by cytoplasmic strands.

(E) Floridean starch is usually associated with the nuclear area of cells and not chloroplasts.

(F) Mitochondria and Golgi bodies are morphologically similar to green algae and angiosperms.

(G) Lamellar reorganization occurs with chloroplast division.

Literature Cited

Ben-Shaul, Yehuda, J. A. Schiff, & H. T. Epstein. 1964. Studies of chloroplast development in *Euglena* VII. Fine structure of the developing plastid. Plant Physiol. **39:** 231-240.

Bischoff, H. W. 1965. Amer. Jour. Phycology (in press).

———, & H. C. Bold. 1964. Phycological studies. IV. The soil algal flora of Enchanted Rock and related algal species. Univ. Tex. Publication No. 6318.

Bouck, G. B. 1962. Chromatophore development, pits and other fine structure in the red alga, *Lomentaria baileyana* (Harv.) Farlow. Jour. Cell Biol. **12:** 553-570.

Brody, M., & A. E. Vatter. 1959. Observations on cellular structures of *Porphyridium cruentum*. Jour. Biophy. Biochem. Cytol. **5:** 289-294.

Dixon, P. S. 1963. The taxonomic implications of the "pit connexions" reported in the *Bangiophycidae*. Taxon **11:** 108-110.

Esau, K. 1963. Ultrastructure of differentiated cells in higher plants. Amer. Jour. Bot. **50:** 495-505.

Fan, K. C. 1960. On pit-connections in the *Bangiophycidae*. Nova Hedwigia **1:** 305-307.

Mollenhauer, H. 1959. Permanganate fixation of plant cells. Jour. Biophy. Biochem. Cytol. **6:** 431-436.

———. 1964. Plastic embedding mixtures for use in electron microscopy. Jour. Stain Technol. **39**: 111-114.

Millonig, G. 1961. A modified procedure for lead staining of thin sections. Jour. Biophy. Biochem. Cytol. **11**: 736-739.

Myers, A., R. D. Preston, & G. W. Ripley. 1956. Fine structure in the red algae. I. X-ray and electron microscope investigation of *Griffithsia flocculosa*. Proc. Roy. Soc. London **144**: 450-459.

———. 1959. An electron microscope investigation into the structure of the floridean pit. Ann. Bot. **23**: 257-260.

Nichols, H. W. 1964. Culture and developmental morphology of *Compsopogon coeruleus* (Balbis) Mont. Amer. Jour. Bot. **51**: 180-188.

Papenfuss, G. F. 1955. Classification of algae, *In* A Century of progress in the natural sciences, 1853-1953, p. 115-224. San Francisco, Calif. Acad. Sci.

Plumel, M. 1948. Tampon au cacodylate de sodium. Bull. Soc. Chem. Biol. **30**: 129-130.

Ris, H., & W. Plaut. 1962. Ultrastructure of DNA-containing areas in the chloroplast of *Chlamydomonas*. Jour. Cell Biol. **13**: 383-391.

Sager, R. 1962. Streptomycin as a mutagen for non-chromosomal genes. Proc. Nat. Acad. Sci. **48**: 2018-2026.

———, & M. R. Ishida. 1963. The particulate nature of non-chromosomal genes in *Chlamydomonas*. Proc. Nat. Acad. Sci. **50**: 260-269.

Ueda, K. 1961. Structure of plant cells with special reference to lower plants VI. Structure of chloroplasts in algae. Cytologia **26**: 344-358.

Weier, T. E. 1963. Changes in the fine structure of chloroplasts and mitochondria during phylogenetic and ontogenetic development. Amer. Jour. Bot. **50**: 604-611.

Whaley, W. G., H. Mollenhauer, & J. E. Kephart. 1959. The endoplasmic reticulum and the Golgi structure in maize root cells. Jour. Biophy. Biochem. Cytol. **5**: 501-506.

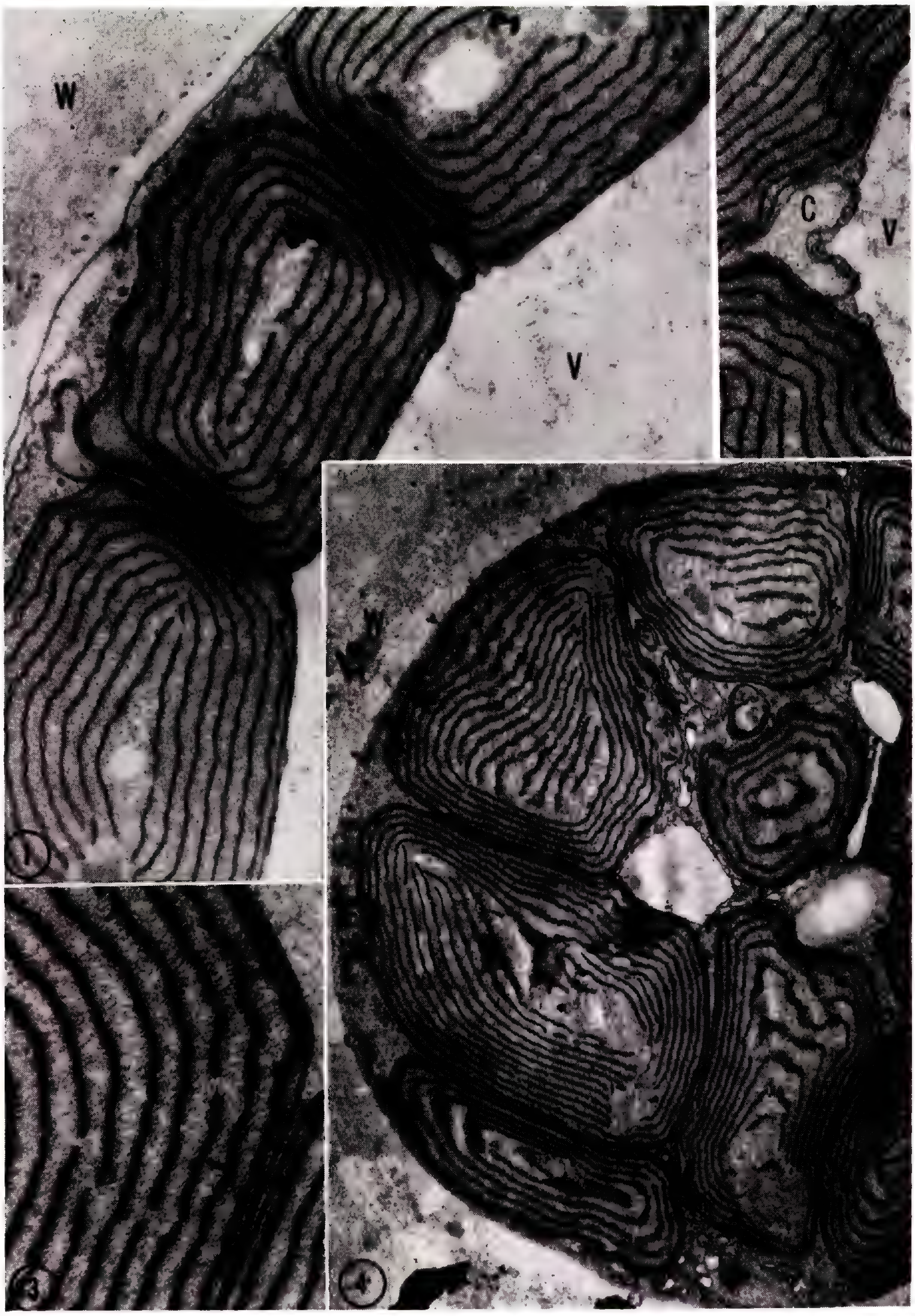


Fig. 1-4. *Compsopogon coeruleus.* Fig. 1. Sections of parietal chloroplasts; ×16,900. Fig. 2. Adjacent chloroplasts with associated membranes; ×32,300. Fig. 3. Section of a single chloroplast showing the regularity of lamellar structures; ×38,000. Fig. 4. Section of a young filament showing closely associated chloroplasts; ×60,000.

Key to Labeling: V = vacuole; W = cell wall; LM = limiting membrane; PP = proplastid; N = nucleus; FS = floridean starch; C = cytoplasm; CL = chloroplast.

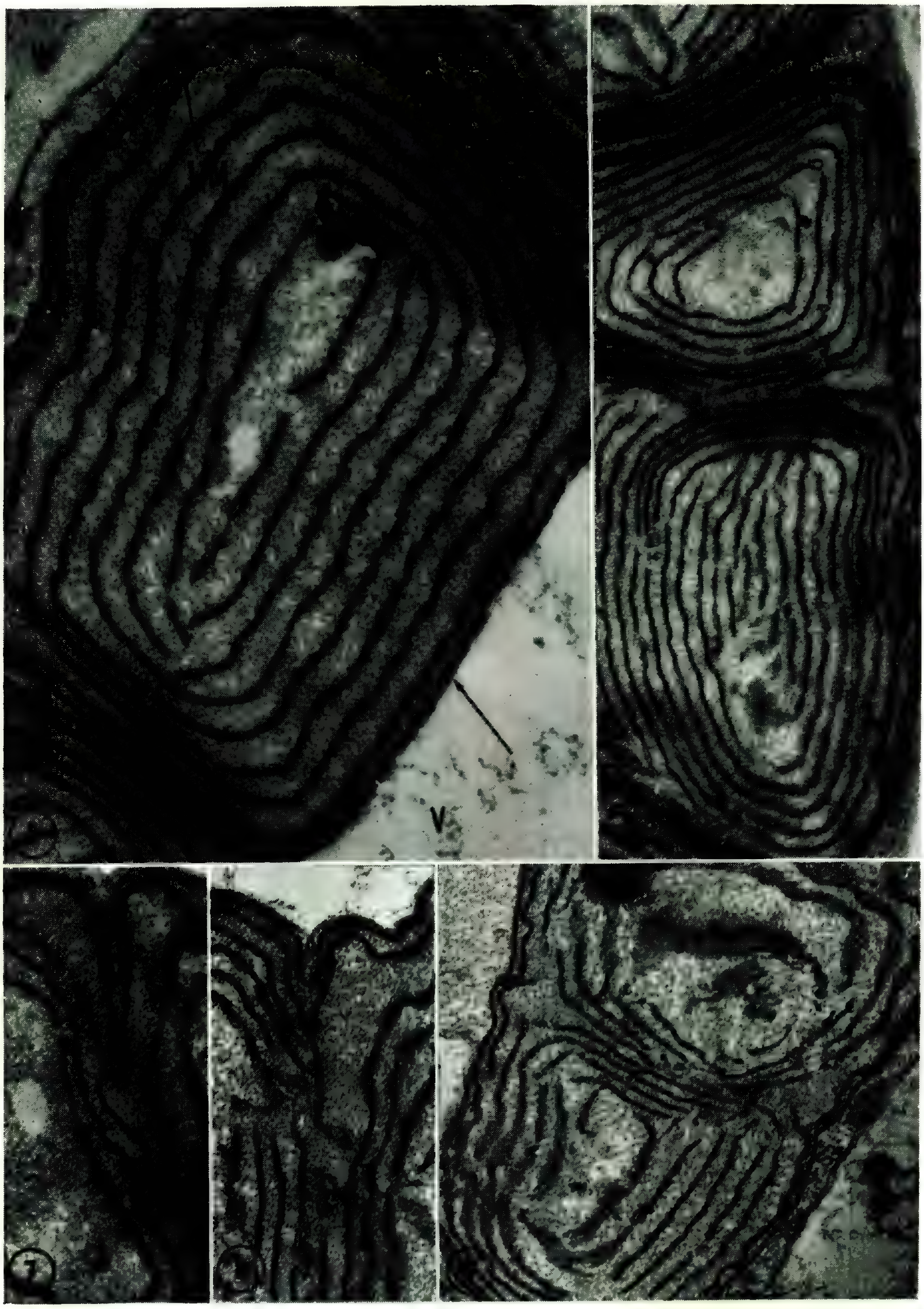


Fig. 5-9. Chloroplasts of *Compsopogon coeruleus*. Fig. 5. Section of a single chloroplast showing double limiting membrane and vacuolar membrane; ×60,300. Fig. 6. Dividing chloroplast in section; ×30,000. Fig. 7. Breaking of lamellar structure in a dividing chloroplast; ×46,300. Fig. 8. Lamellar structures during median division of a chloroplast; ×59,500. Fig. 9. Near-median division of a single chloroplast; ×32,30C. (See Key to Labeling, p. 24)

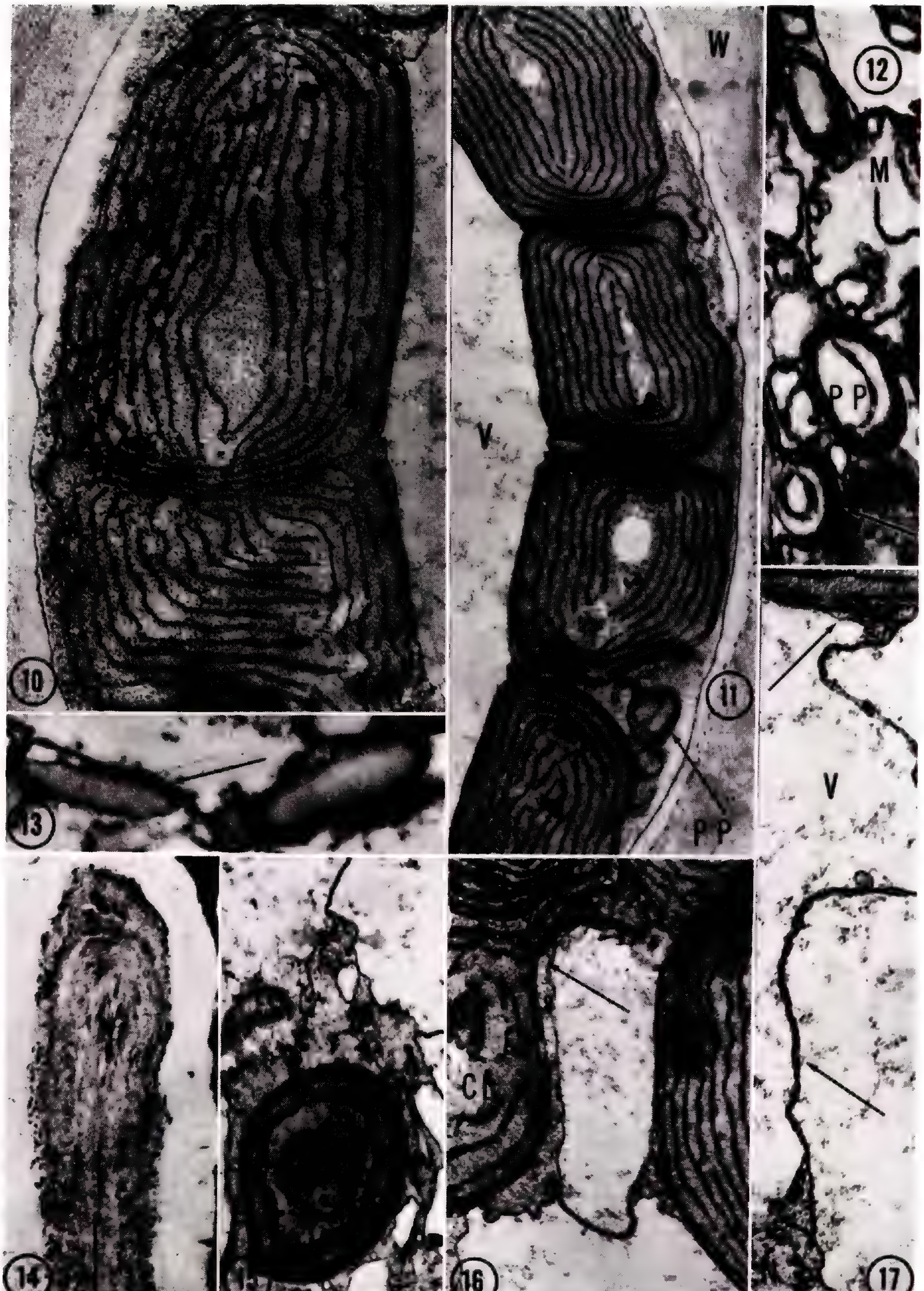


Fig. 10-17. *Compsopogon coeruleus*. Fig. 10. Dividing chloroplast; ×16,150. Fig. 11. Section of chloroplasts showing relationships between chloroplasts, cell walls and vacuole; ×20,000. Fig. 12. Mitochondria and plastids; note the arrow which indicates a proplastid-like segment from a mature chloroplast; ×27,000. Fig. 13. Floridean starch grains and associated vacuolar membranes; ×46,300. Fig. 14. Young developing cell wall. Arrow denotes direction of growth; ×16,150. Fig. 15. Oblique section of a single chloroplast; ×16,150. Fig. 16. Unequal division of a chloroplast with associated vacuole and membranes; ×20,480. Fig. 17. Vacuolar membranes from chloroplast and nuclear areas; ×27,700. (See Key to Labeling, p. 24)

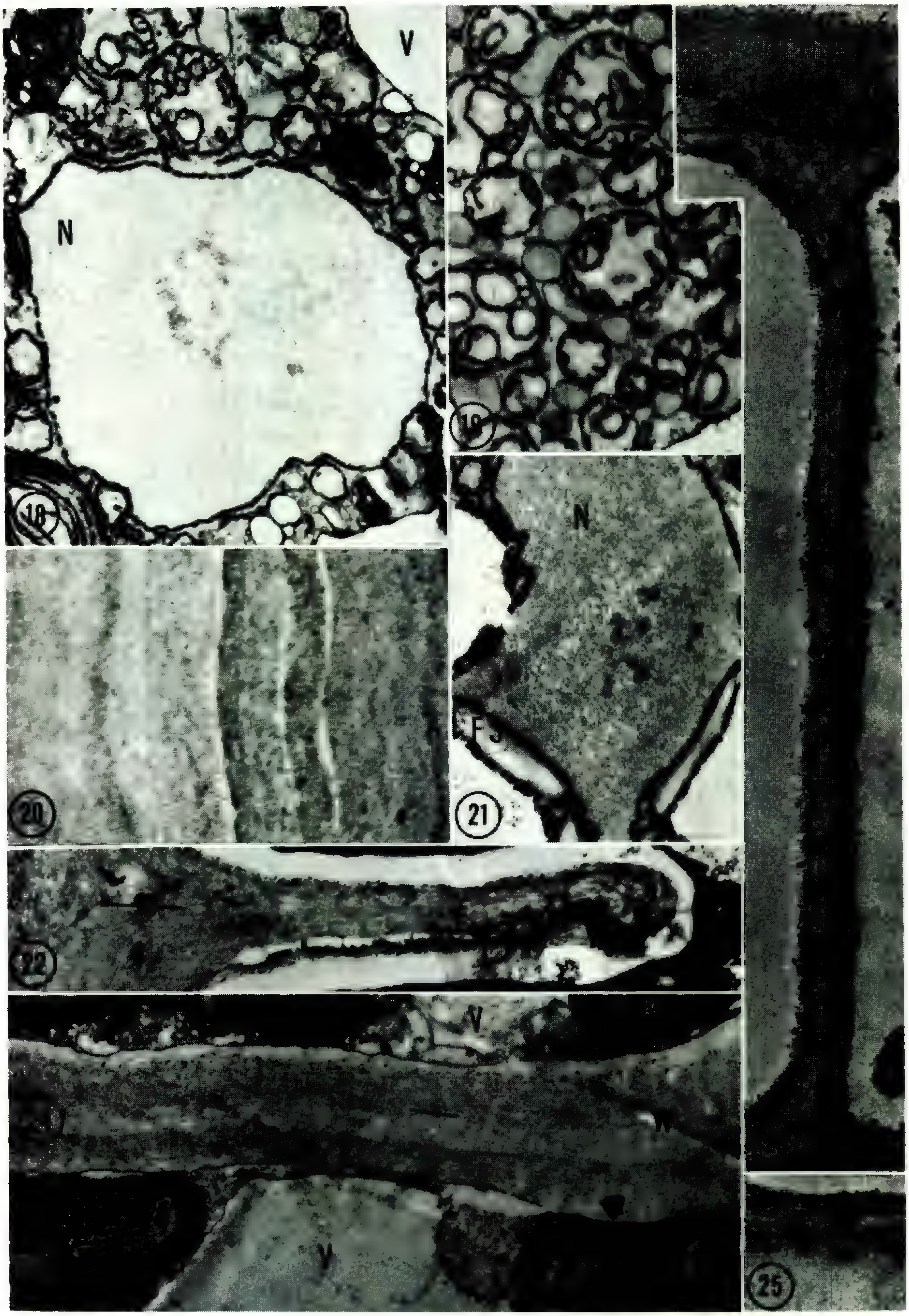


Fig. 18-25. *Compsopogon coeruleus.* Fig. 18. Nucleus with associated mitochondria and Golgi bodies; ×20,000. Fig. 19. Mitochondria from the nuclear area; ×16,150. Fig. 20. Layers of cell wall material in an older cell wall; ×26,000. Fig. 22. Developing cell wall. Arrow denotes direction of growth (longitudinal section of a uniseriate filament); ×10,800. Fig. 23. Complete cell wall deposition, longitudinal section. Arrow denotes 2 layers of outer wall; ×10,800. Fig. 24. Median longitudinal section of a uniseriate filament showing wall between adjacent cells. Note the 3 distinct layers and absence of 'true' pit connections; ×16,150. Fig. 25. Two distinct layers of the outer wall of a cell in a uniseriate filament (longitudinal section); ×10.800. (See Key to Labeling, p. 24)

TWO NEW SPECIES OF DAPHNIPHYLLUM

BY TSENG-CHIENG HUANG[1,2]

Missouri Botanical Garden and Department of Botany, Washington University, St. Louis, Missouri

ABSTRACT

Daphniphyllum woodsonianum from Sumatra and *D. philippinense* from Luzon are described as new. The former is similar to *D. glaucescens* subsp. *scortechinii* (based on *D. scortechinii* Hook. f.) while the latter resembles *D. glaucescens* subsp. *borneense* (based on *D. borneense* Stapf).

Daphniphyllum **woodsonianum** Huang, sp. nov.—Fig. 1.

Folia verticillata vel subverticillata, subsessilia; lamina obovata, oblongo-ovata vel oblongo-obovata, coriacea, venis 7-9. *Inflorescentia* racemiformia. *Flos* masculus sine calyce vel calyce cupuliformi (?) flos femineus cum calyce. *Stamina* 8-11, filamentis longissimis, antheris elliptico-ovatis, apice triangularibus. *Ovarium* ovatum; stigma brevissima.

Shrubs or *trees,* the branchlets round, canaliculate, reddish-brown, the lenticels elliptic, elevate. *Leaves* verticillate or subverticillate, the petioles broadly triangular, very short, thickened at the base, 2 mm long and wide; blades obovate, oblong-ovate to oblong-obovate, the base obtuse, the apex rounded, rarely emarginate to mucronulate, the margins entire, 4-7 cm long, 2.5-4.5 cm wide, coriaceous, shining, smooth, brown on both surfaces, the lateral veins 7-9, thin, elevate-reticulate beneath. *Staminate inflorescences* oblong, 1.5-3 cm long, 0.2 mm wide, the pedicels oblong, 4-7 mm long, 0.1 mm wide; calyx absent or very shallowly cupuliform; stamens 8-11, the filaments oblong, 1.3-2.3 mm long, 0.1 mm wide, the anthers elliptic-ovate, 0.6-0.8 mm long, 0.4-0.5 mm wide, the triangular apex 0.2 mm long and wide. *Pistillate inflorescences* angulate, ca 2.5 cm long, 0.8 mm wide, the pedicels flat, 2-3 mm long, 0.1 mm wide; calyx oblong or obovate-oblong, subentire or with an irregularly divided apex, caducous, 0.4 mm long, 0.3 mm wide; ovary ovate, the stigma short, radiate or revolute.

INDONESIA. N. SUMATRA: Gaju & Alas lands, Paetjoeh Augasan, Aivonac, ridge forest alt 2500 m, *van Steenis 8362* (L, holotype; BO, K, isotypes?), mountain shrubs, alt 2950-3500 m, *van Steenis 8654* (BO, L).

Since both staminate (Kew & Bogor specimens) and pistillate (Leiden specimen) plants were collected by van Steenis under the same number (*8362*), possibly more than one tree was involved, perhaps the species is monoecious, or less likely the specimens were mislabelled.

---

[1] I would like to thank Drs. W. H. Lewis, J. D. Dwyer and A. Robyns for their assistance as well as the curators of the following herbaria for the loan of specimens: A, BM, BO, F, GH, K, L, MO, NY, US.

[2] Present address: Department of Botany, National Taiwan University, Taipei, Taiwan.

ANN. MISSOURI BOT. GARD. **53**(1): 28-31, 1966.

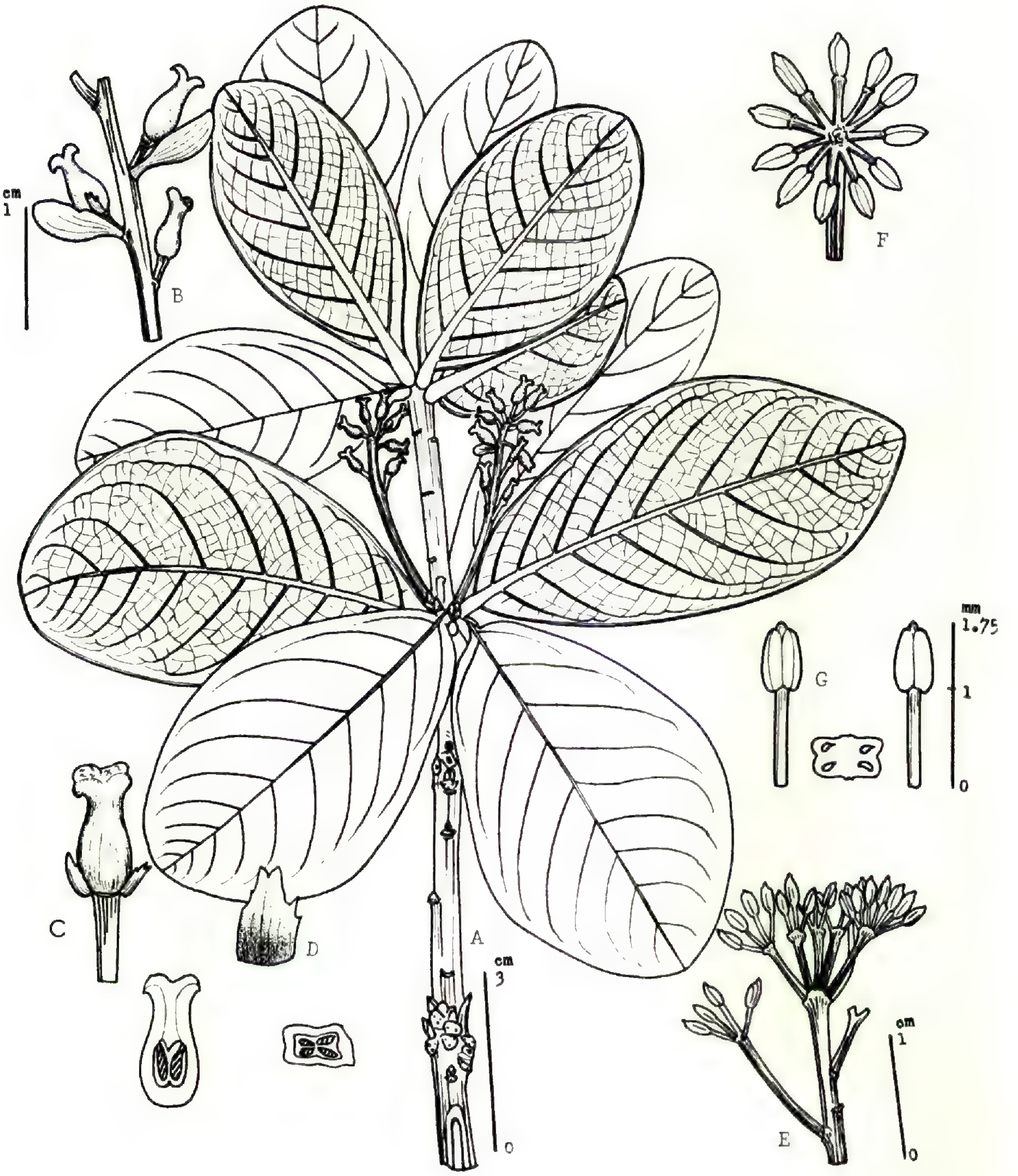


Fig. 1. *Daphniphyllum woodsonianum* Huang. A: Twig with pistillate flowers (*van Steenis 8362*, L); B: Portion of a pistillate inflorescence (*van Steenis 8362*, L); C: Ovary and longitudinal and cross sections of the ovary (*van Steenis 8362*, L); D: Calyx (*van Steenis 8362*, L); E: Staminate inflorescence (*van Steenis 8362*, K); F: Naked staminate flower (*van Steenis 8362*, K); G: Stamen, dorsal and ventral views, and anthers in cross section (*van Steenis 8362*, K).

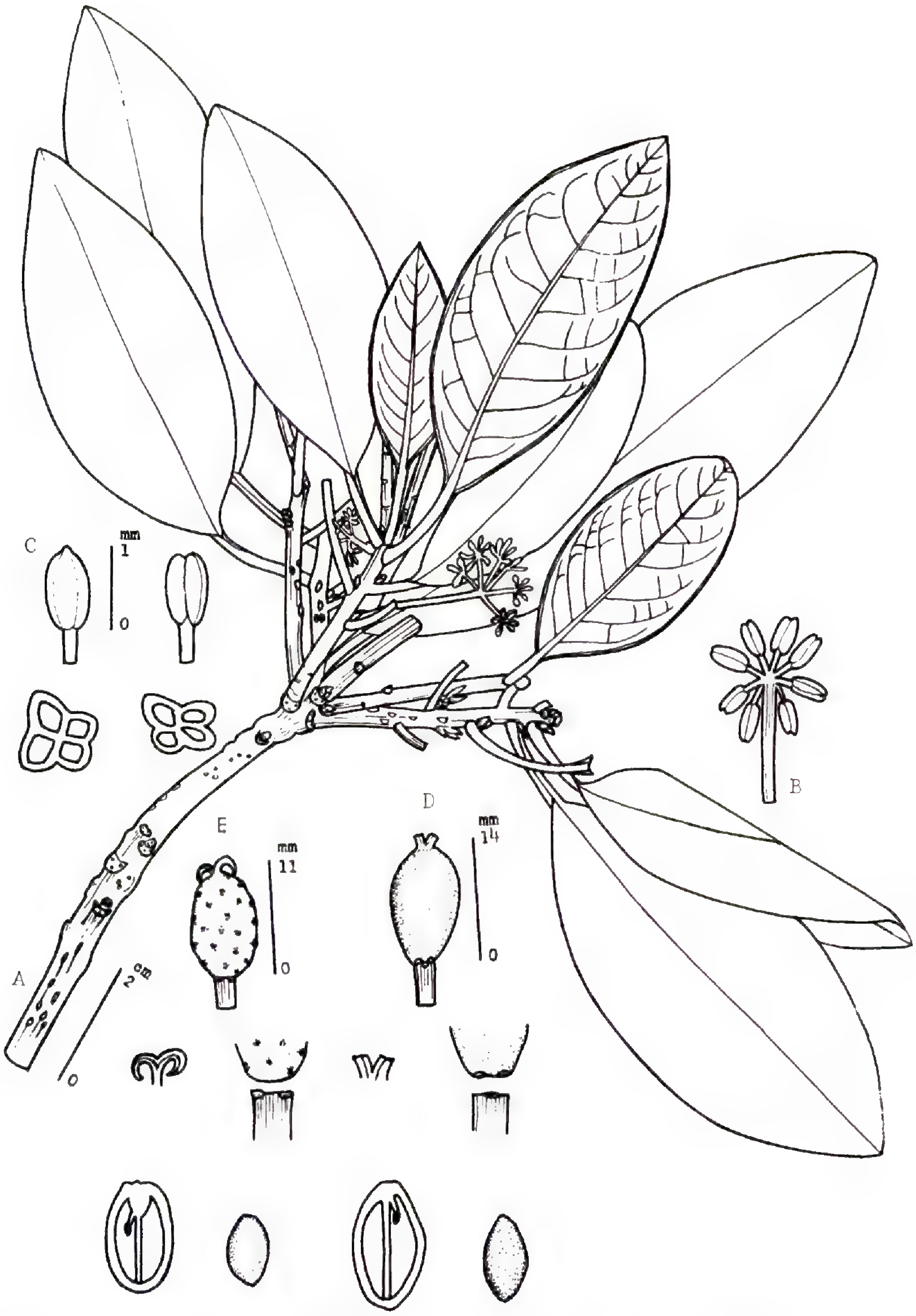


Fig. 2. *Daphniphyllum philippinense* Huang. A: Twig with naked staminate flowers (*Curran et al. 18357*, US); B: Naked staminate flower (*Curran et al. 18357*, US); C: Stamens showing apiculate and emarginate apices and anthers in cross section (*Curran et al. 18357*, US); D: Smooth fruit with divaricate styles, staminodia scars and calyx scars, longitudinal section, and a seed (*Ramos 23478*, F); E: Tuberculate fruit with revolute styles, staminodia scars, longitudinal section, and a seed (*Merrill 1748*, GH).

The texture and shape of leaves of *D. woodsonianum* is very similar to those of *D. glaucescens* subsp. **scortechinii** (Hook. f.) Huang, stat. nov. (*D. scortechinii* Hook. f., Fl. Brit. Ind. **5:** 354, 1887), except for the subsessile and subverticillate arrangement of leaves. In addition, the former differs from the latter by the absence of a calyx in staminate flowers.

The new species is named after the late Dr. R. E. Woodson, Jr.

Daphniphyllum **philippinense** Huang, sp. nov.—Fig. 2.

Folia fasciculata, petiolata; lamina anguste angulato-ovata, coriacea, venis 7-9. *Inflorescentia* racemiformia. *Flos* masculus sine calyce flos femineus sine calyce (?) vel calyce caduco. *Stamina* 5-11, antheris oblongis vel oblongo-ellipticis apiculatis. *Drupa* ellipsoidea vel elliptico-globosa, glabra vel tuberculata; stigma divaricata. *Semina* elliptico-globosa glabraque.

Shrubs or trees, the branchlets round, gray-brown, the lenticels elliptic, rather large, prominent. *Leaves* fasciculate, the petioles triangular, sulcate above, 2-4 cm long, 1.5 mm wide; blades narrowly angular-ovate, the base attenuate, the apex acute or obtuse, the margins revolute, 9-13 cm long, 3-4.5 cm wide, coriaceous, shining, pale green on both surfaces, the veins 7-9, thin, slightly prominent on both surfaces. *Staminate inflorescences* racemiform, flat, ca 3 cm long, 0.1 mm wide, the pedicels 4-7 mm long, 0.1 mm wide, calyx absent; stamens 5-7(-11), the filaments 0.2-0.4 mm long, 0.1 mm wide, the anthers oblong or oblong-elliptic, 0.7-0.8 mm long, 0.5 mm wide, apiculate. *Fruiting* axes racemiform, angulate, 3-8.5 cm long, 1 mm wide, the pedicels angulate, 1-2.5 cm long, 1 mm wide, calyx absent or caducous; staminodia scars and calyx scars (?) prominent in 1-2 whorls; drupes ellipsoidal, elliptic-globose, 10-15 mm long, 6-8 mm in diam, smooth or tuberculate, black, the stigma divaricate. *Seeds* elliptic-globose, smooth, 7 mm long, 5 mm in diam.

PHILIPPINES. LUZON: Benque, Mt Pulog, *Curran, Merritt & Zachokke 18357* (US, holotype), *Merrill 1748* (BM, BO, GH, L, MO, NY); Mancayan to Gaguio, *Ramos & Edano 40478* (A, K, L, US); Camarines, *Ramos 1503* (BM, BO, GH, L, MO, NY); Leyte, Dagami, *Ramos 15235* (BM, K, US); Sorsogon, *Ramos 23478* (A, BM, BO, F, K, L, MO, NY, US).

This new species is related to and perhaps evolved from *D. glaucescens* subsp. **borneense** (Stapf) Huang, stat. nov. (*D. borneense* Stapf, Trans. Linn. Soc., Ser. 2, **4:** 224, 1894) because of their similar leaves and their smooth, ellipsoidal or elliptic-globose drupes. Two different types of fruiting specimens are assigned to this new species for it is not definitely known which type belongs here. The one type (*Merrill 1748*) has ellipsoidal, tuberculate drupes with prominent staminodial scars while the other type (*Ramos 23478*) has ellipsoidal, smooth, drupes with a prominent calyx and staminodial scars.

THE ASIAN GENUS NEANOTIS NOMEN NOVUM (ANOTIS) AND ALLIED TAXA IN THE AMERICAS (RUBIACEAE)[1]

BY WALTER H. LEWIS[2]

Missouri Botanical Garden and Department of Botany, Washington University, St. Louis, Missouri

ABSTRACT

The 14 species of *Anotis* DC. originally included in that genus by de Candolle are all referable to earlier valid genera. All species are native to the New World; none are associated with the Asian genus *Anotis* auct. A new generic name *Neanotis* is proposed for the related but distinct species indigenous to Asia and one section, 28 species, and six varieties are validated under *Neanotis*. All sectional and specific names known under *Anotis* are placed under appropriate genera. In addition, new data from the morphology of the pollen emphasize the discontinuity between the species of *Neanotis* and those of *Hedyotis* (including *Oldenlandia*).

A majority of taxonomists have included the Asian species in the rubiaceous tribe *Hedyotideae* with typically few, peltate, cymbiform seeds and the herbaceous habit under *Anotis* DC. Such was the conclusion of Hooker (1873, 1880) and Schumann (1891) who maintained the genus distinct from *Hedyotis* L. and *Oldenlandia* L. Their treatment generally has been followed in the 20th century, notably by Hutchinson (1916), Hayata (1920), Craib (1932) and Merrill & Metcalf (1937), and additional evidence will be given to illustrate that those species included under *Anotis* are separable from all other Asian members of the complex.

What proved necessary, however, was to expand this study to related taxa in the Americas for world-wide monographers had heretofore credited a few species of *Anotis* to the New World. In fact the genus was described by de Candolle (1830) as wholly American with most of the 14 species he recognized indigenous to South America. Obviously the present concept of *Anotis* differs from that outlined by de Candolle and I found it essential to resolve precisely what species he described in the New World before proceeding to questions involving Asian taxa.

Anotis was divided by de Candolle into three sections: the largest sect. *Ereicotis* DC. having 10 species, one species only in the sect. *Amphiotis* DC. and three species in the sect. *Panetos* (Raf.) DC. (*Panetos* Raf., Ann. Gen. Sci. Phys. **5**: 225, 227, 1820). Nine species of the sect. *Ereicotis* are closely allied and form a homogenous grouping indigenous to the Andes. These are referable to *Arcytophyllum* Willd. ex Schult. & Schult. f. established three years earlier so that in large part *Anotis* and all but one species included under *A.* sect. *Ereicotis* is

---

[1] Supported by Grant No. GB-3825 from the National Science Foundation.

[2] I wish to thank Dr. R. C. Bakhuizen van den Brink of the Rijksherbarium, Leiden, for his careful review of the manuscript.

I am also grateful to the directors and staffs of herbaria (BRIU, F, GH, K, L, S, SING, US) who kindly sent specimens on loan or who extracted material for pollen analysis.

synonymous with *Arcytophyllum.* Excluded from this grouping is *Anotis cervantesii* DC. This species, described from material collected in Mexico (Nova Hispania, *Kunth s.n.*, photo MO from B), has suffruticose stems similar to the other nine species, but differs in fruit, seed and pollen morphology and is *Hedyotis* (*Houstonia*) *wrightii* (A. Gray) Fosb. belonging to an entirely different group of species native to North America. Even earlier than *A. cervantesii,* however, is *Hedyotis pygmaea* Roem. & Schult. based on the same material and described in 1818 so that *H. wrightii,* a name long associated with the species in Mexico, must be replaced by *H. pygmaea.*

The sect. *Amphiotis* consists only of *A. lanceolata* (Poir.) DC., a North American species having much in common with *Hedyotis pygmaea* except that the seeds are fewer and of a different morphology. The species is properly referred to *H. purpurea* (L.) Torrey & Gray var. *calycosa* (A. Gray) Fosb.

The three species included in the sect. *Panetos* are strikingly similar in habit (herbaceous and ± prostrate stems) and leaf morphology (small and rotund), but beyond these vegetative parallelisms de Candolle's assemblage is heteromorphic. *Anotis rotundifolia* (Michx.) DC. is *Hedyotis* (*Houstonia*) *procumbens* (Gmel.) Fosb. native to the southeastern U. S., *A. salzmanni* DC. (*Salzmann s.n.,* type MO) is a native South American species (to Argentina, Brazil, Chile, Paraguay, Uruguay) long known under the later *Oldenlandia thesiifolia* (St.-Hil.) K. Sch. and is referable to *H. salzmannii* (DC.) Steudel. The third species included in this section is *Anotis serpens* (H. B. K.) DC. (lectotype of *Anotis,* cf. Hooker, 1873) which is *Arcytophyllum microphyllum* (Willd. ex Roem. & Schult.) Standl. based on *Houstonia microphylla.* With its angular seeds the species does not appear typical of *Arcytophyllum,* but until a revision of that genus is completed, I prefer not to transfer the species to *Hedyotis, Oldenlandia* or another genus (i.e. *Anotis*).

All 14 species described by de Candolle under *Anotis* can, therefore, be placed with reasonable accuracy in America taxa, namely *Arcytophyllum, Hedyotis* subg. *Edrisia* (Raf.) W. H. Lewis (*Houstonia*) or the pantropical *H.* subg. *Oldenlandia* (L.) Torrey & Gray or *Oldenlandia* L. s.s. No species is known to occur in Asia or to be associated with the large group of Asian species currently grouped under *Anotis.* Moreover, it is clear that de Candolle was not circumscribing Asian elements of this genus for the only species in the Prodromus (1830) typical of *Anotis* of others was placed by him questionably in *Putoria* Pers., a genus far removed in that work from his *Anotis.*

In summary the species of *Anotis* as described by de Candolle (which in this context is illegitimate for the earlier *Panetos* Raf. is given in synonymy) are given as follows together with their correct names:

A. filiformis (Ruiz & Pav.) DC. = *Arcytophyllum filiforme* (Ruiz & Pav.) Standl.;

A. filiformis (Ruiz & Pav.) DC. = *Arcytophyllum filiforme* (Ruiz & Pav.) Standl.;

A. hypnoides (H. B. K.) DC. = *Arcytophyllum bryoides* (Willd. ex Roem. & Schult.) Diels;

A. juniperifolia (Ruiz & Pav.) DC. = *Arcytophyllum juniperifolium* (Ruiz & Pav.) Standl.;

A. microphylla (Willd. ex Roem. & Schult.) DC. = *Arcytophyllum filiforme* (Ruiz & Pav.) Standl.;

A. cervantesii (H. B. K.) DC. = *Hedyotis pygmaea* Roem. & Schult.;

A. thymifolia (Ruiz & Pav.) DC. = *Arcytophyllum thymifolium* (Ruiz & Pav.) Standl.;

A. laricifolia (Cav.) DC. = *Arcytophyllum laricifolium* (Cav.) W. H. Lewis;

A. setosa (Ruiz & Pav.) DC. = *Arcytophyllum setosum* (Ruiz & Pav.) Standl.;

A. ericoides (Willd. ex Roem. & Schult.) DC. = *Arcytophyllum ericoides* (Willd. ex Roem. & Schult.) Standl.;

A. lanceolata (Poir.) DC. = *Hedyotis purpurea* (L.) Torrey & Gray var. *calycosa* (A. Gray) Fosb.;

A. rotundifolia (Michx.) DC. = *Hedyotis procumbens* (Gmel.) Fosb.;

A. salzmanni DC. = *Hedyotis salzmannii* (DC.) Steudel;

A. serpens (H. B. K.) DC. = *Arcytophyllum microphyllum* (Willd. ex Roem. & Schult.) Standl.

Following the taxonomists of the second half of the 19th century and the majority of those in the 20th who recognized *Anotis* as distinct from *Hedyotis* or *Oldenlandia*, a new name is therefore required for *Anotis* in their sense. I propose:

Neanotis W. H. Lewis, nom. nov.

Hedyotis L. sect. *Anotis* sensu Wight & Arn., Prodr. 409, 1834, excl. *Anotis rotundifolia* (Michx.) DC.; Endl., Gen. Pl. 549, 1838, excl. δ *Panetos* (Raf.) Endl. & ε *Ereicotis* (DC.) Endl.

Oldenlandia L. § *Anotis* sensu Miq., Fl. Ind. Bat. **2:** 193, 1857, excl. *Oldenlandia ramosissima* (Blume) Miq.

Anotis sensu Hook. f. in Benth. & Hook. f., Gen. Pl. **2:** 59, 1873, excl. sect. *Serpicula* Hook. f. & sect. *Pterospora* Hook. f., non DC. (Prodr. **4:** 431, 1830).

Distribution: Asia.

Type species: *Neanotis indica* (DC.) W. H. Lewis.

Type collection: *Leschenault s.n.*, Nilgherry, India, G (not seen), widely distributed in IDC Micro-Edition, Candolle Prodromi Herbarium, Fig. 1.

During a routine examination of pollen from among the Asian members of the tribe *Hedyotideae* several species were segregated by their unique pollen morphology. These included all species of *Neanotis* as listed in Appendix 1, i.e. the majority of species formerly known under *Anotis* auct. non DC. Some species included under *Anotis* auct. have also been known under *Hedyotis* and *Oldenlandia,* but the morphology of the pollen of *Neanotis* on the one hand and of *Hedyotis* and *Oldenlandia* on the other is so different that there is a distinct line of demarcation between them.

Fig. 1. *Neanotis indica* (DC.) W. H. Lewis var. *indica* (*Putoria? indica* DC.), type species of *Neanotis; Leschenault s.n.*, Nilgherry, India, type collection reproduced from IDC Micro-Edition, Candolle Prodromi Herbarium.

The main distinguishing characters of the pollen based on the species listed in Appendix 1 are summarized as follows:

Hedyotis (Fig. 2-4)	*Neanotis* (Fig. 5-6)
3- to 4-aperturate, average of all species 3.3.	(5-)6- to 12-aperturate, average of all species 8.5.
colpus long, $\frac{2}{3}$ to $\frac{4}{5}$ length of polar axis.	colpus short (brevicolpate), $\frac{1}{5}$ to $\frac{1}{4}$ length of polar axis.
os narrow, but distinct with breadth only $\frac{1}{8}$ to $\frac{1}{5}$ length of colpus.	os wide, but vague (because of thick and coarse sexine) with breadth $\frac{1}{2}$ to $\frac{4}{5}$ length of colpus.
sexine $\pm$ thin, ca 1.5-2μ.	sexine thick, ca 3-5.5μ and often thicker at the equator.
reticulation fine to medium with fine bacula and muri.	reticulation very coarse with large bacula and muri.
grain subspheroidal to usually prolate.	grain subspheroidal to usually oblate.

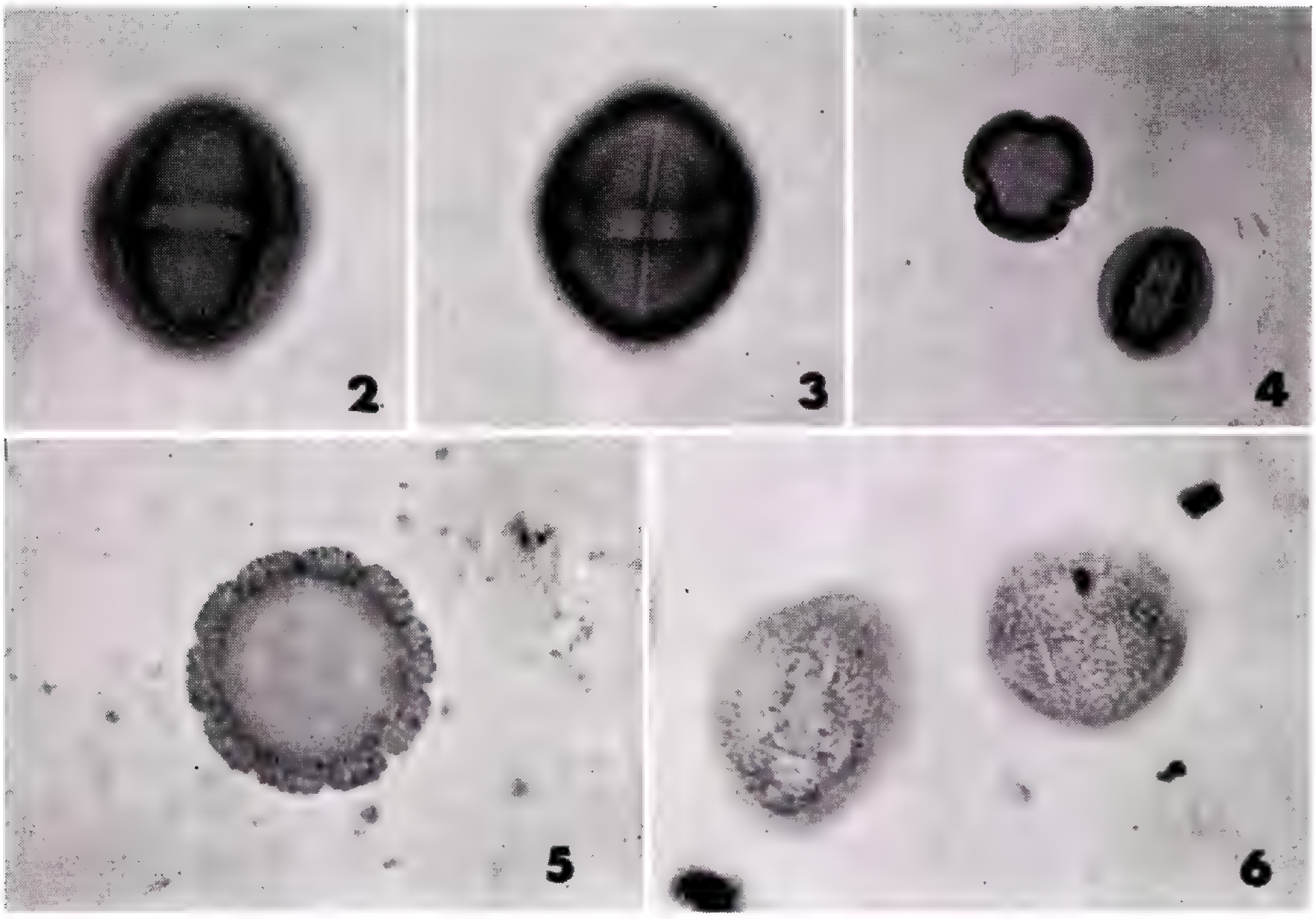


Fig. 2-6. Pollen of *Hedyotis* and *Neanotis*. ×400. Fig. 2-3. *Hedyotis buxifolia* Bedd., *Fischer* 3558 (K), two equatorial focuses of same grain; Fig. 2 showing two colpi and the synclinorate os; Fig. 3 showing one long colpus and the synclinorate os. Fig. 4. *H. cinereo-viridis* Thw., *C. P.* 95 (K), showing one grain in equatroial view with two (of three) colpi and ora, and a second in polar view with three colpi. Fig. 5. *N. foetida* (Hook. f.) W. H. Lewis, *Hohenacker* 586 (K), showing 10 colpi and a thick sexine in polar view. Fig. 6. *N. decipiens* (Hook. f.) W. H. Lewis, *Wight s.n.* (K), showing several of many brevicolpi and indistinctly the broad synclinorate os in near equatorial views.

By six characters, involving most of the major criteria by which pollen is generally distinguished, the species of *Hedyotis* (including *Oldenlandia*) and *Neanotis* are separable. No other species examined in the tribe from Asia and Australia has a pollen morphology remotely similar to that known for *Neanotis* whereas that typical of *Hedyotis* is common to the tribe as a whole not only in Asia and Australia but also in Africa (Lewis, 1965a). In South and Central America (south of Mexico) and the West Indies the pollen of species in the tribe is with one exception similar to that described for *Hedyotis*. This emphasizes the distinct difference between the species grouped under *Anotis* by de Candolle, which are all of the *Hedyotis* type, and those in Asia now known under *Neanotis*. The single exception is the pollen of *Hedyotis callitrichoides* (Griseb.) W. H. Lewis, briefly referred to and incorrectly figured by Bremekamp (1952, p. 269, 297), a species native to Mexico and the West Indies and probably of recent introduction into western Africa. Like *Neanotis*, the pollen is polycolporate (8-aperturate) and usually oblate, but differs by its long colpi, narrow ora, and thin sexine ± finely reticulated as noted for species of *Hedyotis*. Palynologically the species is unique for *Hedyotis* and its position in the genus remains uncertain. Most species of *Hedyotis* in North

America also differ in pollen morphology from that typical of the *Hedyotideae* (Lewis, 1965b), although along different lines from that of *Neanotis* where multiplication of apertures rather than of their individual complexity is the most obvious specialization.

Palynologically, therefore, the species of *Neanotis* are distinct not only from their allies in Asia but also from all members of the tribe *Hedyotideae* known elsewhere. This newly described set of characters lends added support to the generally accepted position that this group of species must be set apart from *Hedyotis* s.l.

No attempt is made here to be monographic although such a study of the genus is needed. With available material I have examined as many as possible of the specific and subspecific taxa transferred below to *Neanotis*. Needed transfers may not be complete, however, and some have been omitted due to lack of specimens. Conversely, I find that several species such as *N. boerhaavioides, N. formosana,* and *N. kwangtungensis* are similar in vegetative characters as well as their (atypical) seed morphology. A revisionary treatment may ultimately show that a more conservative approach is necessary.

Below are proposed one section, 28 species, and six varieties under *Neanotis*.

Neanotis W. H. Lewis sect. **Patzea** (Schlecht. ex Hook. f.) W. H. Lewis, comb. nov., type species *N. wightiana* (Wall. ex Wight & Arn.) W. H. Lewis.

Anotis sect. *Patzea* Schlecht. ex Hook. f. in Benth. & Hook. f., Gen. Pl. **2:** 59, 1873.

A. sect. *Patria* Boerl., Handl. **2:** 53, 1891.

Neanotis **boerhaavioides** (Hance) W. H. Lewis, comb. nov.

Hedyotis boerhaavioides Hance, Jour. Bot. **8:** 73, 1870.

Anotis boerhaavioides (Hance) Maxim., Bull. Acad. Imp. Sc. St. Pétersb. **29:** 165, 1883.

Neanotis **calycina** (Wall. ex Hook. f.) W. H. Lewis, comb. nov.

Anotis calycina Wall. ex Hook. f, Fl. Brit. Ind. **3:** 73, 1880 (*Hedyotis calycina* Wall., Cat. no. 878, 1829, nom. nud.; Wight & Arn., Prodr. 409, 1834, nom. nud.).

Neanotis **carnosa** (Dalz.) W. H. Lewis, comb. nov.

Hedyotis carnosa Dalz., Hook. Jour. Bot. **2:** 135, 1850.

[3] *Anotis carnosa* (Dalz.) Hook. f., Fl. Brit. Ind. **3:** 74, 1880.

Neanotis **decipiens** (Hook. f.) W. H. Lewis, comb. nov.

Anotis decipiens Hook. f., Fl. Brit Ind. **3:** 72, 1880.

---

[3] This is the first of many combinations under *Anotis* ascribed to Hook. f. in Benth. & Hook. f., Gen. Pl. **2:** 59-60, 1873, in the *Index Kewensis. Hedyotis carnosa,* for example, was only listed under *Anotis* in the *Genera Plantarum* and Article 33 of the *International Code of Botanical Nomenclature* expressly states that such a combination is not validly published. Fortunately, however, many invalid combinations were validly published by Hooker in the *Flora of British India* seven years later.

Neanotis **foetida** (Hook. f.) W. H. Lewis, comb. nov.
Hedyotis foetida Dalz., Hook. Jour. Bot. **2:** 134, 1850, non (Forst.) J. E. Smith in Rees (Cyclop. **17,** 1811).
Anotin foetida Hook. f., Fl. Brit. Ind. **3:** 74, 1880.

Neanotis **formosana** (Hayata) W. H. Lewis, comb. nov.
Anotis formosana Hayata, Ic. Pl. Formos. **9:** 54, 1920.

Neanotis **gracilis** (Hook. f.) W. H. Lewis, comb. nov.
Anotis gracilis Hook. f., Fl. Brit Ind. **3:** 71, 1880.

Neanotis **hirsuta** (L. f.) W. H. Lewis, comb. nov.
Oldenlandia hirsuta L. f., Suppl. Pl. Syst. Veg. 127, 1781.
Hedyotis hirsuta (L. f.) J. E. Smith in Rees, Cyclop. **17,** 1811.
H. lindleyana Hook. ex Wight & Arn., Prodr. 409, 1834, nom. subnud.
Oldenlandia japonica Miq., Ann. Mus. Lugd.-Bat.: **3:** 109, 1867.
Hedyotis stipulata R. Br. in Wall. [Cat. no. 863a, 1829, no. 6195, 1831-32, nom. nud.] ex Hook. f, Fl. Brit. Ind. **3:** 63, 1880.
Anotis hirsuta (L. f.) Boerl., **2:** 126, 1891 (superfluously made by Miq. ex Backer & van Slooten, Geïllustr. Handb. Theeonkr. 203, 1924, and by Hochr., Candollea **5:** 246, 1934).

Neanotis hirsuta var. **glabrior** (Miq.) W. H. Lewis, comb. nov.
Hedyotis capitata Blume, Bijdr. Fl. Nederl. Ind. 973, 1826, non Lam. (Encycl. Méth. Bot. **3:** 80, 1789).
Oldenlandia hirsuta var. *glabrior* Miq., Fl. Ind. Bat. **2:** 194, 1857.
Anotis hirsuta var. *glabrior* (Miq.) Hochr., Candollea **5:** 246, 1934.

Neanotis hirsuta var. **glabricalycina** (Honda) W. H. Lewis, comb. nov.
Oldenlandia hirsuta var. *glabricalycina* Honda, Bot. Mag. Tokyo **53:** 333, 1939.
Hedyotis lindleyana Hook. ex Wight & Arn. var. *glabricalycina* (Honda) Hara, Jour. Jap. Bot. **18:** 89, 1942.

Neanotis hirsuta var. **yakusimensis** (Masamune) W. H. Lewis, comb. nov.
Oldenlandia yakusimensis Masamune, Jour. Soc. Trop. Agr. Taiwan **3:** 393, 1931.
Hedyotis lindleyana var. *yakusimensis* (Masamune) Hara, Jour. Jap. Bot. **18:** 89, 1942.

Neanotis **hondae** (Hara) W. H. Lewis, comb. nov.
Oldenlandia hirsuta L. f. var. *glabra* Honda, Bot. Mag. Tokyo **45:** 2, 1931.
O. glabra (Honda) Honda, loc. cit. **47:** 297, 1933, non O. Ktze. (Rev. Gen. Pl. **1:** 292, 1891).
Hedyotis hondae Hara, Jour. Jap. Bot. **18:** 90, 1942.

Neanotis **indica** (DC.) W. H. Lewis, comb. nov.
Putoria? indica DC., Prodr. **4:** 577, 1830.
Hedyotis leschenaultiana Wall. [Cat. no. 1298, 1829, nom. nud.] ex Wight & Arn., Prodr. 411, 1834.
Anotis leschenaultiana (Wall. ex Wight & Arn.) Hook. f., Fl. Brit. Ind. **3:** 72, 1880.

Neanotis indica var. **affinis** (Hook. f.) W. H. Lewis, comb. nov.
Hedyotis affinis Wall. [Cat. no. 1297, 1829, nom. nud.] ex Wight & Arn., Prodr. 411, 1834, non Roem. & Schult. in L. (Syst. Veg., ed. 15, **3:** 194, 1818).
Anotis leschenaultiana var. *affinis* Hook. f., Fl. Brit. Ind. **3:** 72, 1880.

Neanotis indica var. **deltoidea** (Wall. ex Wight & Arn.) W. H. Lewis, comb. nov.
Hedyotis deltoidea Wall. [Cat. no. 1296, 1829, nom. nud.] ex Wight & Arn., Prodr. 410, 1834.
Anotis leschenaultiana var. *deltoidea* (Wall. ex Wight & Arn.) Hook. f., Fl. Brit. Ind. **3:** 72, 1880.

Neanotis **ingrata** (Wall. ex Hook. f.) W. H. Lewis, comb. nov.
Anotis ingrata Wall. ex Hook. f., Fl. Brit. Ind. **3:** 71, 1880 (*Hedyotis ingrata* Wall., Cat. no. 863, 1829, nom. nud.).

Neanotis **kwangtungensis** (Merrill & Metcalf) W. H. Lewis, comb. nov.
Anotis kwangtungensis Merrill & Metcalf, Lingnan Sci. Jour. **16:** 177, 1937.

Neanotis **lancifolia** (Hook. f.) W. H. Lewis, comb. nov.
Hedyotis lancifolia Dalz., Hook. Jour. Bot. **2:** 135, non Schum. in Schum. & Thonn. (Beskr. Guin. Pl. **1:** 92, 1827).
Anotis lancifolia Hook. f., Fl. Brit. Ind. **3:** 73, 1880.

Neanotis **longiflora** W. H. Lewis, nom. nov.
Anotis longiflora Hutch., Kew Bull. **1916:** 35, 1916, non Benth. (Pl. Hartw. 23, 1839).

Neanotis **monosperma** (Wall. ex Wight & Arn.) W. H. Lewis, comb. nov.
Hedyotis monosperma Wall. [Cat. no. 1295, 1829, nom. nud.] ex Wight & Arn., Prodr. 410, 1834.
Oldenlandia mysorensis Wall. [Cat. no. 882, 1829, nom. nud.] ex G. Don, Gen. Syst. Gard. Bot. **3:** 531, 1834.
Anotis monosperma (Wall. ex Wight & Arn.) Hook f., Fl. Brit. Ind. **3:** 75, 1880.

Neanotis **montholoni** (Hook. f.) W. H. Lewis, comb. nov.
Anotis montholoni Hook. f., Fl. Brit. Ind. **3:** 73, 1880.

Neanotis **nummularia** (Arn.) W. H. Lewis, comb. nov.
Hedyotis nummularia Arn., Pugill. Pl. Ind. Or. 23, 1836.
Anotis nummularia (Arn.) Hook. f., Fl. Brit. Ind. **3:** 75, 1880.

Neanotis **nummulariformis** (Arn.) W. H. Lewis, comb. nov.
Hedyotis nummulariformis Arn., Pugill. Pl. Ind. Or. 23, 1836.
Anotis nummulariformis (Arn.) Trimen, Syst. Cat. 42, 1885.

Neanotis **oxyphylla** (G. Don) W. H. Lewis, comb. nov.
Oldenlandia oxyphylla G. Don, Gen. Syst. Gard. Bot. **3:** 531, 1834.
Anotis oxyphylla (G. Don) Hook. f., Fl. Brit. Ind. **3:** 72, 1880.

Neanotis **prainiana** (W. A. Talbot) W. H. Lewis, comb. nov.
Anotis prainiana W. A. Talbot, Jour. Bombay Nat. Hist. Soc. **11:** 237, 1897.

Neanotis **quadrilocularis** (Thw.) W. H. Lewis, comb. nov.
Hedyotis quadrilocularis Thw., Enum. Pl. Zeyl. 144, 1859.
Anotis quadrilocularis (Thw.) Hook. f., Fl. Brit. Ind. **3:** 74, 1880.

Neanotis **rheedei** (Wall. ex Wight & Arn.) W. H. Lewis, comb. nov.
Hedyotis rheedei Wall. [Cat. no. 1294, 1829, nom. nud.] ex Wight & Arn., Prodr. 409, 1834.
H. latifolia Dalz., Hook. Jour. Bot. **2:** 133, 1850.
Anotis rheedei (Wall. ex Wight & Arn.) Hook. f., Fl. Brit. Ind. **3:** 73, 1880.

Neanotis **richardiana** (Arn.) W. H. Lewis, comb. nov.
Hedyotis richardiana Arn., Pugill. Pl. Ind. Or. 22, 1836.
Anotis richardiana (Arn.) Hook. f., Fl. Brit. Ind. **3:** 75, 1880.

Neanotis **ritchiei** (Hook. f.) W. H. Lewis, comb. nov.
Anotis ritchiei Hook. f., Fl. Brit. Ind. **3:** 74, 1880.

Neanotis **thwaitesiana** (Hance) W. H. Lewis, comb. nov.
Hedyotis thwaitesiana Hance, Jour. Bot. **6:** 298, 1868.
Anotis thwaitesiana (Hance) Maxim., Bull. Acad. Imp. Sc. St. Pétersb. **29:** 165, 1883.

Neanotis **trimera** (Craib) W. H. Lewis, comb. nov.
Anotis trimera Craib, Fl. Siam. Enum. **2:** 59, 1932; Kew Bull. **1932:** 127, 1932.

Neanotis **urophylla** (Wall. ex Wight & Arn.) W. H. Lewis, comb. nov.
Hedyotis urophylla Wall. [Cat. no. 6197, 1831-32, nom. nud.] ex Wight & Arn., Prodr. 409, 1834, nom. subnud.
Anotis urophylla (Wall. ex Wight & Arn.) Hook. f., Fl. Brit. Ind. **3:** 72, 1880.

Neanotis **wightiana** (Wall. ex Wight & Arn.) W. H. Lewis, comb. nov.
Hedyotis wightiana Wall. [Cat. no. 6194, 1831-32, nom. nud.] ex Wight & Arn., Prodr. 410, 1834.
Anotis wightiana (Wall. ex Wight & Arn.) Hook. f., Fl. Brit. Ind. **3:** 75, 1880.

Neanotis wightiana var. **compressa** (Wall. ex G. Don) W. H. Lewis, comb. nov.
Spermacoce compressa Wall. [Cat. no. 6187, 1831-32, nom. nud.] ex G. Don, Gen. Syst. Gard. Bot. **3:** 621, 1834.
Hedyotis wightiana var. *β* Wight & Arn., Prodr. 410, 1834.
Anotis wightiana var. *compressa* (Wall. ex G. Don) Craib, Fl. Siam. Enum. **2:** 59, 1932.

The number of sectional and specific names known under *Anotis* is large and I feel that it is essential to consider all of them and to at least tentatively place them under appropriate taxa. In a few instances a considerable list of synonymy is

also given particularly when the names are newly placed in that position. The sections known under *Anotis* are given first followed by the specific epithets alphabetically.

Anotis sect. *Amphiotis* DC., Prodr. **4:** 433, 1830. = *Hedyotis* subg. *Edrisia* (Raf.) W. H. Lewis.

Anotis sect. Ereicotis DC., Prodr. **4:** 431, 1830. =*Arcytophyllum* Willd. ex Schult. & Schult. f., pro parte, and *Hedyotis* subg. *Edrisia* (Raf.) W. H. Lewis, pro parte.

Anotis sect. *Euanotis* Hook. f. in Benth. & Hook. f., Gen. Pl. **2:** 59, 1873. = *Neanotis* W. H. Lewis sect. *Neanotis.*

Anotis sect. *Panetos* (Raf.) DC., Prodr. **4:** 433, 1830. = *Arcytophyllum* Willd. ex Schult. & Schult. f., pro parte, *Hedyotis* subg. *Edrisia* (Raf.) W. H. Lewis, pro parte, and *Hedyotis* subg. *Oldenlandia* (L.) Torrey & Gray or *Oldenlandia* L., pro parte.

Anotis sect. *Patria* Boerl., Handl. **2:** 53, 1891. = *Neanotis* sect. *Patzea* (Schlecht. ex Hook. f.) W. H. Lewis.

Anotis sect. *Patzea* Schlecht. ex Hook. f. in Benth. & Hook. f., Gen. Pl. **2:** 59, 1873. = *Neanotis* sect. *Patzea* (Schlecht. ex Hook. f.) W. H. Lewis.

Anotis sect. *Pterospora* Hook. f. in Benth. & Hook. f., Gen. Pl. **2:** 60, 1873. = *Hedyotis* L. (or *Oldenlandia* L.).

Anotis sect. *Serpicula* Hook. f. in Benth. & Hook. f., Gen. Pl. **2:** 60, 1873. = *Arcytophyllum* Willd. ex Schult. & Schult f.

Anotis affinis, nom. illegit.[4] = *Neanotis indica* var. *affinis* (Hook. f.) W. H. Lewis.

Anotis arnottiana (Miq.) Hochr., Candollea **5:** 245, 1934. = *Neanotis indica* (DC.) W. H. Lewis.

Anotis blumeana (DC.) Korth., Nederl. Kruid. Arch. **2**(2): 150, 1851. = *Oldenlandia biflora* L., Sp. Pl. 119, 1753.

Anotis boerhaavioides (Hance) Maxim., Bull. Acad. Imp. Sc. St. Pétersb. **29:** 165, 1883. = *Neanotis boerhaavioides* (Hance) W. H. Lewis.

Anotis calycina Wall. ex Hook. f., Fl. Brit. Ind. **3:** 73, 1880. = *Neanotis calycina* (Wall. ex Hook. f.) W. H Lewis.

Anotis capitata (Lam.) Korth., Nederl. Kruid. Arch. **2**(2): 151, 1851. = *Hedyotis capitata* Lam., Encycl. Méth. Bot. **3:** 80, 1789.

Anotis carnosa (Dalz.) Hook. f., Fl. Brit. Ind. **3:** 74, 1880. = *Neanotis carnosa* (Dalz.) W. H. Lewis.

Anotis cervantesii (H. B. K.) DC., Prodr. **4:** 432, 1830. = *Hedyotis pygmaea* Roem. & Schult. in L., Syst. Veg., ed. 15, **3:** 526, 1818 [*Hedyotis pumila* Willd. ex Roem. & Schult. in L., loc. cit., pro syn., non L. f. (Suppl. Pl. Syst. Veg. 119, 1781); *H. cervantesii* H. B. K., Nov. Gen. Sp. Pl. **3:** 396, 1820; *Houstonia wrightii*

[4] This and several other names indicated simply by nom. illegit. are given in the *Index Kewensis* and elsewhere as legitimate binomials, but unlike most combinations under *Anotis* attributed to Hook. f. in Benth. & Hook. f., Gen. Pl. **2:** 59-60, 1873, which were later validated (cf. footnote 3), these names remain illegitimate.

A. Gray, Proc. Amer. Acad. **17:** 202, 1882; *Hedyotis wrightii* (A. Gray) Fosb., Lloydia **4:** 290, 1941.]

Anotis chrysotricha Paliban, Bull. Herb. Boiss., sér. 2, **6:** 20, 1906. = *Hedyotis chrysotricha* (Paliban) Merrill, Lingnan Sci. Jour. **7:** 322, 1931.

Anotis ciliolosa G. Don, Gen. Syst. Gard. Bot. **3:** 535, 1834. = *Hedyotis canadensis* (Willd. ex Roem. & Schult.) Fobs., Virginia Jour. Sci. **2:** 110, 1941.

Anotis coerulea (L.) G. Don, Gen. Syst. Gard. Bot. **3:** 535, 1834. = *Hedyotis caerulea* (L.) Hook., Fl. Bor. Amer. **1:** 286, 1833.

Anotis conferta (Ruiz & Pav.) DC., Prodr. **4:** 431, 1830. = *Arcytophyllum filiforme* (Ruiz & Pav.) Standl., Field Mus. Nat. Hist., Bot. Ser., **11:** 183, 1936.

Anotis corymbifera Backer ex van Steenis, Bull. Jard. Bot. Buitenz., sér. 3, **13:** 246, 1934, nom. nud. = *Neanotis calycina* (Wall. ex Hook. f.) W. H. Lewis.

Anotis decipiens Hook. f., Fl. Brit. Ind. **3:** 72, 1880. = *Neanotis decipiens* (Hook. f.) W. H. Lewis.

Anotis dentelloides Cham. in Steudel, Nom. Bot., ed. 2, **1:** 101, 1840, nom. nud. pro syn. = *Hedyotis salzmannii* (DC.) Steudel, Nom. Bot., ed. 2, **1:** 728, 1841.

Anotis ericoides (Willd. ex Roem. & Schult.) DC., Prodr. **4:** 433, 1830. = *Arcytophyllum ericoides* (Willd. ex Roem. & Schult.) Standl., Field Mus. Nat. Hist., Bot. Ser., **11:** 182, 1936.

Anotis filiformis (Ruiz & Pav.) DC., Prodr. **4:** 431, 1830. = *Arcytophyllum filiforme* (Ruiz & Pav.) Standl., Field Mus. Nat. Hist., Bot. Ser., **11:** 183, 1936.

Anotis findlaysoniana, nom. illegit. (cf. footnote 4). = *Neanotis wightiana* (Wall. ex Wight & Arn.) W. H. Lewis.

Anotis foetida Hook. f., Fl. Brit. Ind. **3:** 74, 1880. = *Neanotis foetida* (Hook. f.) W. H. Lewis.

Anotis formosana Hayata, Ic. Pl. Formos. **9:** 54, 1920. = *Neanotis formosana* (Hayata) W. H. Lewis.

Anotis gentianoides Walp., Repert. **4:** 230, 1847, nom. illegit. An erroneous index name referring to *Hedyotis* (*Anotis*) *gentianoides* Endl. in Walpers Repert. **2:** 495, 1843; ascribed to Walpers in the *Index Kewensis* and later placed by Standley (Fl. N. Amer. **32:** 30, 1918) in synonymy as a legitimate binomial. = *Hedyotis caerulea* (L.) Hook., Fl. Bor. Amer. **1:** 286, 1833.

Anotis gracilis Hook. f., Fl. Brit. Ind. **3:** 71, 1880. = *Neanotis gracilis* (Hook. f.) W. H. Lewis.

Anotis hirsuta (L. f.) Boerl., Handl. **2:** 126, 1891. = *Neanotis hirsuta* (L. f.) W. H. Lewis.

Anotis hypnoides (H. B. K.) DC., Prodr. **4:** 432, 1830. = *Arcytophyllum bryoides* (Willd. ex Roem. & Schult.) Diels, Biblioth. Bot. **29**(116): 149, 1937. [*Houstonia bryoides* Willd. ex Roem. & Schult. in L., Syst. Veg., ed. 15, **3:** 527, 1818; *Hedyotis hypnoides* H. B. K., Nov. Gen. Sp. Pl. **3:** 389, 1820; *Arcytophyllum confertum* (Ruiz & Pav.) Standl. var. *bryoides* (Willd. ex Roem. & Schult.) Standl., Field Mus. Nat. Hist., Bot. Ser., **7:** 206, 1931.]

Anotis ingrata Wall. ex Hook f., Fl. Brit. Ind. **3:** 71, 1880. = *Neanotis ingrata* (Wall. ex Hook. f.) W. H. Lewis.

Anotis juniperifolia (Ruiz & Pav.) DC., Prodr. **4:** 432, 1830. = *Arcytophyllum juniperifolium* (Ruiz & Pav.) Standl., Field Mus. Nat. Hist., Bot. Ser., **7:** 207, 1931.

Anotis kwangtungensis Merrill & Metcalf, Lingnan Sci. Jour. **16:** 177, 1937. = *Neanotis kwangtungensis* (Merrill & Metcalf) W. H. Lewis.

Anotis lanceolata (Poir.) DC., Prodr. **4:** 433, 1830. = *Hedyotis purpurea* (L.) Torrey & Gray var. *calycosa* (A. Gray) Fosb., Castanea **19:** 33, 1954.

Anotis lancifolia Hook. f., Fl. Brit. Ind. **3:** 73, 1880. = *Neanotis lancifolia* (Hook. f.) W. H. Lewis.

Anotis laricifolia (Cav.) DC., Prodr. **4:** 432, 1830. = *Arcytophyllum laricifolium* (Cav.) W. H. Lewis, Ann. Missouri Bot. Gard. **53:** 110, 1966.

Anotis lechleriana Schlecht., Linnaea **28:** 488, 1856. = *Arcytophyllum filiforme* (Ruiz & Pav.) Standl., Field Mus. Nat. Hist., Bot. Ser., **11:** 183, 1936.

Anotis leschenaultiana (Wall. ex Wight & Arn.) Hook. f., Fl. Brit. Ind. **3:** 72, 1880. = *Neanotis indica* (DC.) W. H. Lewis.

Anotis longiflora Benth., Pl. Hartw. 23, 1839. = *Bouvardia multiflora* (Cav.) Schult. & Schult. f., Mant. Vol. Ter. Syst. Veg. L. (ed. Roem. & Schult.) 118, 1827.

Anotis longiflora Hutch., Kew Bull. **1916:** 35, 1916, non Benth. (Pl. Hartw. 23, 1839). = *Neanotis longiflora* W. H. Lewis.

Anotis microphylla (Willd. ex Roem. & Schult.) DC., Prodr. **4:** 432, 1830. = *Arcytophyllum filiforme* (Ruiz & Pav.) Standl., Field Mus. Nat. Hist., Bot. Ser., **11:** 183, 1936.

Anotis ? minahassae Koorders in Koorders & Schum., Syst. Verz. **3:** 119, 1914, nom. nud. = not known.

Anotis mitrasacmoides (F. Muell.) Domin, Biblioth. Bot. **22**(89): 1170, 1929 (incorrectly ascribed to Benth. & Hook. f., Gen. Pl. **2:** 60, 1873). = *Hedyotis mitrasacmoides* F. Muell., Fragm. **4:** 37, 1863.

Anotis monosperma (Wall. ex Wight & Arn.) Hook. f., Fl. Brit. Ind. **3:** 75, 1880. = *Neanotis monosperma* (Wall. ex Wight & Arn.) W. H. Lewis.

Anotis montholoni Hook. f., Fl. Brit. Ind. **3:** 73, 1880. =*Neanotis montholoni* (Hook. f.) W. H. Lewis.

Anotis nummularia (Arn.) Hook. f., Fl. Brit. Ind. **3:** 75, 1880. = *Neanotis nummularia* (Arn.) W. H. Lewis.

Anotis nummulariformis (Arn.) Trimen, Syst. Cat. 42, 1885. = *Neanotis nummulariformis* (Arn.) W. H. Lewis.

Anotis oxyphylla (G. Don) Hook. f., Fl. Brit. Ind. **3:** 72, 1880. = *Neanotis oxyphylla* (G. Don) W. H. Lewis.

Anotis papuana Lauterb. in K. Sch. & Lauterb., Nachtr. Fl. Deutsch Südsee 391, 1905. = *Neanotis hirsuta* (L. f.) W. H. Lewis.

Anotis pilifera Schlecht., Linnaea **28:** 487, 1856. = *Arcytophyllum filiforme* (Ruiz & Pav.) Standl., Field Mus. Nat. Hist., Bot. Ser., **11:** 183, 1936.

Anotis prainiana W. A. Talbot, Jour. Bombay Nat. Hist. Soc. **11:** 237, 1897. = *Neanotis prainiana* (W. A. Talbot) W. H. Lewis.

Anotis pterospora (F. Muell.) K. Sch. in Engler & Prantl, Nat. Pflanzenfam. IV. **4:** 27, 1891. = *Hedyotis pterospora* F. Muell., Fragm. **4:** 40, 1863.

Anotis purpurea (L.) G. Don, Gen. Syst. Gard. Bot. **3:** 535, 1834. = *Hedyotis purpurea* (L.) Torrey & Gray, Fl. N. Amer. **2:** 40, 1841.

Anotis quadrilocularis (Thw.) Hook. f., Fl. Brit. Ind. **3:** 74, 1880. = *Neanotis quadrilocularis* (Thw.) W. H. Lewis.

Anotis repens K. Sch. in Engler & Prantl, Nat. Pflanzenfam. IV. **4:** 22, *fig. 8H*, 1891, in error for *A. serpens* (H.B.K.) DC.

Anotis rheedei (Wall. ex Wight & Arn.) Hook. f., Fl. Brit. Ind. **3:** 73, 1880. = *Neanotis rheedei* (Wall. ex Wight & Arn.) W. H. Lewis.

Anotis richardiana (Arn.) Hook. f., Fl. Brit. Ind. **3:** 75, 1880. = *Neanotis richardiana* (Arn.) W. H. Lewis.

Anotis ritchiei Hook. f., Fl. Brit. Ind. **3:** 74, 1880. = *Neanotis ritchiei* (Hook. f.) W. H. Lewis.

Anotis rotundifolia (Michx.) DC., Prodr. **4:** 433, 1830. = *Hedyotis procumbens* (Gmel.) Fosb., Castanea **19:** 32, 1954.

Anotis salzmanni DC., Prodr. **4:** 433, 1830. = *Hedyotis salzmannii* (DC.) Steudel, Nom. Bot., ed. 2, **1:** 728, 1841. [*Hedyotis muscosa* St.-Hil., Voy. int. Brésil, Partie 2, Tom **1:** 396, 1833; *H. thesiifolia* St.-Hil., loc. cit. 397; *H. perpusilla* Hook. & Arn., Hook. Bot. Misc. **3:** 359, 1833; *H. pilosa* Poepp. & Endl., Nov. Gen. Sp. Pl. **3:** 30, *t. 235*, 1844; *Oldenlandia thesiifolia* (St.-Hil.) K. Sch. in Mart., Fl. Bras. **6**(6): 269, 1889; *Hedyotis dasycarpa* O. Ktze. ex K. Sch., loc. cit. 270, nom. nud. pro syn.; *H. palustris* Casar. ex K. Sch., loc. cit., nom. nud. pro syn.; *Oldenlandia salzmanni,* nom. illegit., Index Kewensis **2:** 336, 1895.]

Anotis scleranthoides (F. Muell.) Domin, Biblioth. Bot. **22**(89): 1170, 1929. = *Hedyotis scleranthoides* F. Muell., Fragm. **4:** 39, 1863.

Anotis serpens (H. B. K.) DC., Prodr. **4:** 433, 1830. = *Arcytophyllum microphyllum* (Willd. ex Roem. & Schult.) Standl., Field Mus. Nat. Hist., Bot. Ser., **7:** 207, 1931. [*Houstonia microphylla* Willd. ex Roem. & Schult. in L., Syst. Veg., ed. 15, **3:** 527, 1818, non *Hedyotis microphylla* Willd. ex Roem. & Schult. in L. (loc. cit. 526), nec *Oldenlandia microphylla* De Wild. & Th. Dur. (Ann. Mus. Congo, sér. 2, **2:** 28, 1900); *Hedyotis serpens* H. B. K., Nov. Gen. Sp. Pl. **3:** 390, *t. 289*, 1820.]

Anotis serpyllifolia (Michx.) G. Don, Gen. Syst. Gard. Bot. **3:** 535, 1834. = *Hedyotis michauxii* Fosb., Amer. Midl. Nat. **29:** 786, 1943.

Anotis setosa (Ruiz & Pav.) DC., Prodr. **4:** 432, 1830. = *Arcytophyllum setosum* (Ruiz & Pav.) Schlecht., Linnaea **28:** 489, 1856.

Anotis tenella (Pursh) G. Don, Gen. Syst. Gard. Bot. **3:** 535, 1834. = *Hedyotis michauxii* Fosb., Amer. Midl. Nat. **29:** 786, 1943.

Anotis teysmanniana, nom. illegit. (cf. footnote 4); *Oldenlandia teysmanniana* Miq., Fl. Ind. Bat. **2:** 354, 1857. = *Neanotis wightiana* (Wall. ex Wight & Arn.) W. H. Lewis.

Anotis thwaitesiana (Hance) Maxim., Bull. Acad. Imp. Sc. St. Pétersb. **29:** 165, 1883. = *Neanotis thwaitesiana* (Hance) W. H. Lewis.

Anotis thymifolia (Ruiz & Pav.) DC., Prodr. **4:** 432, 1830. = *Arcytophyllum thymifolium* (Ruiz & Pav.) Standl., Field Mus. Nat. Hist., Bot. Ser., **7:** 208, 1931.

Anotis trachymenoides (F. Muell.) Domin, Biblioth. Bot. **22**(89): 1170, 1929. = *Hedyotis trachymenoides* F. Muell., Fragm. **4**: 39, 1863.

Anotis trimera Craib, Fl. Siam. Enum. **2**: 59, 1932. = *Neanotis trimera* (Craib) W. H. Lewis.

Anotis urophylla (Wall. ex Wight & Arn.) Hook. f., Fl. Brit. Ind. **3**: 72, 1880. = *Neanotis urophylla* (Wall. ex Wight & Arn.) W. H. Lewis.

Anotis wightiana (Wall. ex Wight & Arn.) Hook. f., Fl. Brit. Ind. **3**: 75, 1880. = *Neanotis wightiana* (Wall. ex Wight & Arn.) W. H. Lewis.

Literature Cited

Bremekamp, C. E. B. 1952. The African species of *Oldenlandia* L. sensu Hiern et K. Schumann. Verh. Kon. Nederl. Akad. Wet., Afd. Natuurk., sect. 2, **48**: 1-297.

Candolle, A. P., de. 1830. *Anotis*, p. 431-433, *In* Prodromus systematis naturalis regni vegetabilis. Vol. 4.

Craib, W. G. 1932. *Anotis*, p. 59, *In* Florae Siamensis enumeratio. Vol. 2.

Erdtman, G. 1952. Pollen morphology and plant taxonomy. Angiosperms. Almqvist and Wiksell, Stockholm.

Hayata, B. 1920. *Anotis*, p. 54, *In* Icones plantarum Formosanarum. Vol. 9.

Hooker, J. D. 1873. *Hedyotideae*, p. 53-64, *In* Bentham & Hooker, Genera plantarum. Vol. 2.

————. 1880. *Hedyotis, Oldenlandia,* & *Anotis*, p. 49-76, *In* Flora of British India. Vol. 3.

Hutchinson, J. 1916. *Anotis longiflora, In* V.—Decades Kewenses. Kew Bull. **1916**: 35.

Lewis, W. H. 1965a. Cytopalynological study of African *Hedyotideae* (*Rubiaceae*). Ann. Missouri Bot. Gard. **52**: 182-211.

————. 1965b. Pollen morphology and evolution in *Hedyotis* subgenus *Edrisia* (*Rubiaceae*). Amer. Jour. Bot. **52**: 257-264.

Merrill, E. D. & F. P. Metcalf. 1937. New Kwangtung plants. Lingnan Sci. Jour. **16**: 167-180.

Schumann, K. 1891. *Anotis*, p. 27, *In* Engler & Prantl, Nat. Pflanzenfam. IV. **4**.

Appendix 1

Palynological Procedures and Materials

Whole flowers or mature buds were removed from herbarium specimens and acetolyzed according to the procedure outlined by Erdtman (1952). Some collections were also chlorinated before being mounted in glycerin jelly and sealed with paraffin. A complete set of slides is maintained at the Missouri Botanical Garden (MO) and duplicates of those from which material was received from other herbaria (BRIU, GH, K, L, S, SING, US) will be filed with these institutions.

The species of *Hedyotis* from Asia and Australia and of *Neanotis* studied are listed alphabetically below together with the collector and number, herbarium where specimen is filed, and the country of origin. An attempt has been made to examine pollen from a wide range of morphologically diverse species in each genus. For the large genus *Hedyotis* the following taxa are represented: *H.* sect. *Anotidopsis* Hook. f. (pro parte *Hedyotis*), *H.* sect. *Dimetia* Wight & Arn., *H.* sect. *Diplophragma* Wight & Arn., *H.* sect. *Hedyotis, H.* sect. *Involucrella* Hook. f., and *H.* sect. *Leptopetalum* (Hook & Arn.) Hook. f. as well as a few species of *H.* subg. *Oldenlandia* (L.) Torrey & Gray or *Oldenlandia s.s.*

Hedyotis *acutangula* Champ., *Dahlström 17* (S), Hongkong; *H.* cf. *albo-nervia* Bedd., *Bahadur 616* (MO), India; *H. ampliflora* Hance, *Gressitt 908* (MO), China; *H. apoensis* Elmer, *Elmer 11499* (MO), Philippines; *H. articularis* R. Br. in Wall. ex Wight & Arn., *Gamble 16676* (K), India; *H. auricularia* L., *Tsang 21727* (S), China; *H. benguetensis* Elmer, *Elmer 14281* (MO), Philippines; *H. buxifolia* Bedd., *Fischer 3558* (K), India; *H. caerulescens* F. Muell., *Adams 1253* (BRIU), Australia; *H. capitellata* Wall. ex G. Don, *Lace 5598* (K), Burma; *H.* cf. *capituligera* Hance, *Forrest 25115* (MO), China; *H. chrysotricha* (Paliban) Merrill, *Dunn s.n.* (K), China; *H. cinereo-viridis* Thw., *C. P. 95* (K), Ceylon; *H. congesta* R. Br. in Wall. ex Wight & Arn., *Merrill 7028* (MO), Philippines; *H.* cf. *connata* Wall. ex Hook. f., *Ramos & Edaño,* Bur. Sci. 44122 (SING), Philippines; *H. cyanantha* Kurz (*H. coerulea* Wight & Arn., non *H. caerulea* (L.) Hook.), *Ambo 6878* (K), India; *H. effusa* Hance, *Tsang 21021* (K), China, *Tsang 21044* (S), China; *H. elegans* Wall. ex Hook. f., *Garrett 817* (K), Thailand; *H. foetida* (Forst.) J. E. Smith var. *mariannensis* (Merrill) Fosberg, *Moran 4552* (MO), Guam; *H. fruticosa* L., *Walker 170* (K), Ceylon; *H. galioides* F. Muell., *Burbidge 5955* (MO), Australia; *H. glabra* (Roxb.) Wight & Arn., *Kerr 7652* (K), Thailand; *H. grayi* Hook. f., *Otomo s.n.* (GH), Bonin Islands; *H. hedyotidea* (DC.) Merrill, *Tsang 21291* (S), China; *H. hispida* Retz., *Ramos*, Bur. Sci. 13572 (MO), Philippines, *Wenzel 349* (MO), Philippines; *H. irosinensis* Elmer, *Elmer 17394* (MO), Philippines; *H. lancea* Thunb. ex Maxim., *Tso & Tsiang 2001* (K); *H. lessertiana* Arn., *Gardner 349* (K), Ceylon; *H. macrostemum* Hook. & Arn., *Fortune 53* (MO), Hongkong; *H. matthewii* Dunn (*H. acuminatissima* Merrill), *Gressitt 1631* (MO), China; *H. mellii* Tutcher, *Gressitt 1305* (MO), China; *H. membranacea* Thw., *Kunjyar 3452* (K), India; *H. mitrasacmoides* F. Muell., *Pedley 958* (BRIU), *Specht 232* (US), *Specht 300* (K), all Australia; *H. mollis* Wall. ex G. Don, *Ridley s.n.* (K), Malaya; *H. monocephala* R. Br. in Wall. ex Hook. f., Herb. E India Co. no. 2884 (K), E Pakistan?; *H. nantoensis* Hayata, *Sasaki s.n.* (MO), Taiwan; *H. nicobarensis* W. H. Lewis, *McClelland s.n.* (herb. Hooker) (K), Burma, *Moolmain 375* (K), Burma; *H. ovata* Thunb. ex Maxim., *Lau 208* (K), China; *H. parryi* Hance, *Sampson s.n.* (K), China; *H. patens* Ridley, no collector given *16078* (K), Malaya; *H. platystipula* Merrill, *Tsang 24649* (MO), China; *H. rigida* (Blume) Miq., *Merrill 9214* (MO), Philippines; *H. scandens* Roxb., *Haines 4589* (K), India; *H. scleranthoides* F. Muell., *Cole s.n.* (BRIU), Australia; *H. stylosa* R. Br. in Wall. ex Wight & Arn., *Saulière 401* (K), India; *H. tenuipes* Hemsley, *Gressitt 1684* (MO), China; *H. trinervia* (Retz.) Roem. & Schult., *Ridley 8047* (SING), Singapore; *H. uncinella* Hook. & Arn., *Howell 70* (K), China; *H. vestita* R. Br. in Wall. ex G. Don, *Vaughan 522* (K), Malaya, *Wenzel 3276* (MO), Philippines; *H. vinelliflora* Blume, *Elmer 15155* (MO), Philippines.

Neanotis *boerhaavioides* (Hance) W. H. Lewis, *Steward et al. 830* (S), China; *N. calycina* (Wall. ex Hook. f.) W. H. Lewis, *Sedgwick & Bell 7605* (K), India, *Yü 17672* (GH), China; *N. carnosa* (Dalz.) W. H. Lewis, *Schlagintweit 445* (GH), India; *N. decipiens* (Hook. f.) W. H. Lewis, *Barnes 130* (GH), India, *Wight s.n.* (K), India; *N. foetida* (Hook. f.) W. H. Lewis, *Hohenacker 586* (K), India; *N. formosana* (Hayata) W. H. Lewis, *Susuki 620(670?)* (MO), Taiwan; *N. hondae* (Hara)W. H. Lewis, *Ohwi & Koyama*, NSM 279 (MO), Japan; *N. hirsuta* (L. f.) W. H. Lewis (including *Hedyotis lindleyana* Hook. ex Wight & Arn. and *H. stipulata* R. Br. in Wall. ex Hook. f.), *Henry 10043* (MO), China, *Holstvoogd 423* (L), Indonesia, *Johnston & Johnston 94* (SING), Malaya; *N. indica* (DC.) W. H. Lewis, *Kjellberg s.n.* (S), Indonesia; *N. indica* var. *affinis* (Hook. f.) W. H. Lewis, *Bembower 189* (MO), India, *Wight 1385* (GH), India; *N. ingrata* (Hook. f.) W. H. Lewis, *Henry 7366* (GH), China; *N. lancifolia* (Hook f.) W. H. Lewis, *Santapau 11263* (K), India; *N. longiflora* W. H. Lewis, *Saulière 292* (K), India; *N. monosperma* (Wall. ex Wight & Arn.) W. H. Lewis, *Hooker f. & Thomson s.n.* (GH), India; *N. montholoni* (Hook. f.) W. H. Lewis, *Sedgwick & Bell 6183* (K), India; *N. nummularia* (Arn.) W. H. Lewis, *Gardner 383* (K), Ceylon; *N. oxyphylla* (G. Don) W. H. Lewis, *Hooker 772* (K), China; *N. rheedei* (Wall. ex Wight & Arn.) W. H. Lewis, *Canara 6* (K), Malaysia; *N. richardiana* (Arn.) W. H. Lewis, *Hooker f. & Thomson 34* (GH), India, *Macrae 288* (GH), Ceylon; *N. urophylla* (Wall. ex Wight & Arn.) W. H. Lewis, *Griffith 2900* (GH), E Pakistan; *N. wightiana* (Wall. ex Wight & Arn.) W. H. Lewis, *Hooker f. & Thomson s.n.* (K), India.

REVISION OF MEXICAN AND CENTRAL AMERICAN SAURAUIA (DILLENIACEAE)[1]

BY GORDON E. HUNTER
Murray State College, Murray, Kentucky

ABSTRACT

Two new species of *Saurauia* (*S. pustulata* and *S. squamifructa*) are reported among 22 recognized from Mexico and Central America. The species are divided into four taxonomic series based on the prominence of the tertiary veins of the leaves, the distribution of trichomes on the sepals and the pubescence of the ovary. Trichomes are recognized as useful for identifying species and a key to the various trichome types occurring in *Saurauia* is provided. The morphology of the versatile anthers of *Saurauia* is discussed. The dehiscence of the anthers is interpreted as basal and extrorse by rimiform pores. The similarities between *Saurauia* and the *Ericales*, especially the *Clethraceae*, are stressed.

The revision and morphological studies are based upon the study of herbarium specimens from 11 important herbaria. These include most of the type specimens as well as most of the specimens annotated by Buscalioni in an earlier revision from 1912-1927.

INTRODUCTION

Saurauia, a widespread tropical genus of flowering plants with about 65 species in the western hemisphere alone, is an important but puzzling element of the tropical American flora. Its distribution is continuous from central Mexico in the north to Chile in the south. Principally, the genus consists of localized populations of subalpine trees and shrubs, but species adapted to lower elevations and having rather broad distributions also are known.

The only revision of the American species of *Saurauia* (Buscalioni, 1912-1927) was completed before sufficient collections were available to show the geographical and natural relationship of the populations. In the mildest of criticisms directed at Buscalioni's revision by workers on tropical American floras, Macbride (1956, p. 678) observes that: "The most recent account of these strikingly attractive plants is lacking in organization and presentation, but one may admire the author's inherent ability and interest, which prompted his studies, probably under difficulties. In any case specific characters to this day are not understood. . . ."

In view of the fact that no contemporary taxonomic treatment of the American species of *Saurauia* has been generally acceptable to botanists, it has become urgent to restudy the specimens cited by Buscalioni, together with the many more recent collections. It is the hope of the writer to extend his studies to include the South American species in the near future.

Saurauia has been divided into a number of series based on the vestiture of the leaves (Buscalioni, 1912; Diels, 1922; Gilg & Werdermann, 1925). This has led to considerable confusion since descriptive terms generally applied to epidermal emergences have never been standardized. Terms have been carelessly used with subjective connotations and without adequately describing them. "Strigose," "seri-

[1] Submitted in partial fulfillment for the Doctor of Philosophy degree at Washington University in affiliation with the Missouri Botanical Garden.

ANN. MISSOURI BOT. GARD. **53**(1):47-89, 1966.

ceous," "villous," etc. may refer to a type of hair, on the one hand, or to a particular condition or aspect of hairiness, on the other. When the diminutive is used, the reader is uncertain whether it is being implied that the vestiture is less dense or whether the individual trichomes are smaller. More important is the fact that the hairiness of the leaves of American *Saurauia* often varies considerably from one population of a species to another. The Guatemalan population, called *S. veneficorum* by Standley & Steyermark (1947), is quite hairy and would certainly have been placed in his series *Strigosae* by Buscalioni; but *S. waldheimia* Busc., based on a nearly glabrous collection from Nicaragua, was included in his series *Oligotrichae*. The two are undoubtedly the same species; they both have the same type of reduced inflorescence, leaves conspicuously villous in the axils of the secondary veins, the same type of sepal vestiture and they both have pubescent ovaries, a rare feature in American *Saurauia*. Similar variability has been found in the pubescence of the leaves of *S. veraguasensis, S. selerorum* and *S. scabrida*.

In place of foliar pubescence, used primarily by Buscalioni to define his taxonomic sections and series, the combination of leaf venation, distributional patterns of sepal pubescence and the presence or absence of pubescence on the ovary have been emphasized. Nevertheless, the types of trichomes occurring on the various organs of the plants are useful in defining the species; therefore, a rather exhaustive treatment is given them in the following pages.

Limits of Variation

Habit: The Mexican and Central American species of *Saurauia* are mostly small trees and shrubs. Two species, *S. laevigata* and *S. seibertii*, however, reach the respectable height of 75-100 feet. The leaves are frequently crowded at the ends of low, spreading, crooked branches. The straight hollowed stems of some of the shrubby species, notably, *S. veraguasensis* of Honduras, are used as blowguns by the natives.

Leaves: The primary division of the key to the series is based on the venation of the leaves. In some species, the tertiary veins jut out from the lower surface of the blade and are more prominent than the lesser reticulum; in others they are immersed and scarcely distinguishable from the lesser reticulum. Only the highly variable *S. waldheimia*, which is easily identified by its pubescent ovary, has leaves which in some specimens fall into the former category and in other specimens fall into the latter. The leaves vary considerably in size from specimen to specimen in the same species. The smallest, 7-10 cm long, are found in a Guatemalan population of *S. waldheimia*. The largest, which may extend beyond the length of the standard herbarium sheet, are found in *S. scabrida*. While it may be said that in general the larger-leaved species of Mexican and Central American *Saurauia* are more hairy and the smaller-leaved species often more or less glabrous, there is considerable overlapping with regard to these two characters. The texture may vary from coriaceous to membranaceous. Leaf shape is so limited within the genus, narrowly elliptical to broadly obovate, and often so variable within the various species that it is of little use in delimiting species.

Inflorescences: That the inflorescence is a complicated phase of the branching of the shoot system is clearly demonstrated in the North American species of *Saurauia.* Following the pattern of the vegetative axis, branching in the inflorescence is spiral. This pattern continues to the ultimate branches. The bracts may be foliaceous, linear, triangular or subulate. Because the upper and smaller are irregular in their orientation, they are of little help in analysis; therefore, one must depend solely on the order of development of the flowers. If the ultimate divisions of many-flowered inflorescences are examined at early stages of development, the secund orientation of buds along scorpioid axis can clearly be seen. Lower flowers along this axis are earlier in their development; thus, the ultimate division is a cincinnus. Although frequently described as a "panicle," the inflorescence of *Saurauia* is obviously a thyrse composed of scorpioid cymes.

Flowers: Except for the usually tetramerous flowers of *S. laevigata,* flowers of *Saurauia* are normally pentamerous. Although stamen number may vary from as low as 13 in *S. conzattii* to as high as 52 in *S. rubiformis,* studies on an Asian *Saurauia* by Brown (1935) suggest that the androecium, too, is basically pentamerous. He noted that the initial stamen primordia in flowers of *S. subspinosa* appear as five mounds of tissue alternating with the petals. Occasional flowers may be found in which the imbricate sepal is partially fused with the adjacent outer sepal. Petals may show a similar fusion. The flowers of *S. leucocarpa* are highly variable, the floral whorls varying in number independently. Flowers from the same inflorescence of this species may have 4-6 sepals, 4-6 petals, and 3-5 carpels. The petals vary in color from white to pink, are fused at the base, more or less oblong to obovate, obtuse at the apex. The margins are entire or incised near the apex in one or more places.

Calyx: All pentamerous flowers of *Saurauia* are quincuncial in the aestivation of the sepals. Two sepals have their entire outer surfaces exposed in the bud; two sepals are almost entirely enclosed with a narrow triangular portion of their outer surface exposed. The fifth sepal is imbricate with about half its outer surface exposed and the other half covered in the bud. The outer sepals are usually ovate or elliptic in outline. More variable, the inner two sepals may be ovate, obovate, elliptic or nearly circular. The exposed half of the imbricate sepal is shaped like the outer sepals and the covered half is shaped like the inner; thus, it is generally asymmetrical. Tetramerous flowers have two outer opposed sepals enclosing, in the bud, two inner opposed sepals. As in the pentamerous flowers, the two inner sepals have a narrow triangular portion exposed in the bud. In both tetramerous and pentamerous flowers the two inner sepals and the imbricate sepal are slightly larger than the two outer.

The distribution of trichomes on the persistent sepals is a reliable and a convenient diagnostic feature of Mexican and Central American *Saurauia.* Some species have sepals which are glabrous over the entire inner surface of the sepals, other species have sepals pubescent over the entire inner surface, and yet another group of species have sepals only partially invested with pubescence. These three groups may be subdivided on the basis of the distribution of the vestiture on the outer surface of the sepals. The outer surface may be (1) glabrous, (2)

pubescent only on the parts exposed in the bud, (3) glabrous on the parts exposed in the bud and pubescent on the parts covered in the bud or (4) 2 kinds of pubescence may be present on the parts exposed in the bud and in this case the parts covered in the bud may be either glabrous or pubescent. The presence of stellate hairs near the articulation of the calyx makes further distinctions possible. Although the margins of the sepals of most species are ciliate, a few are not. In the keys and descriptions which follow, surface vestiture is described separately from marginal vestiture; thus, sepals may be described as both glabrous and ciliate.

The types of trichomes present on the sepals contribute further to classification of Mexican and Central American *Saurauia*. The emergences occurring on the inner surface and the outer surface covered in the bud are stellate types. These are also present on the outer surfaces exposed in the bud when the vestiture is mixed. In addition, hirsute, strigose and shaggy induments occur on the surfaces exposed in the bud.

Epidermal Emergences: One of the most striking features of many species of *Saurauia* is their extreme hairiness. The leaves, petioles, growing points, young branches and all parts of the inflorescence may be densely beset with trichomes. Some species, on the other hand, may be practically glabrous; nevertheless, trichomes of some sort occur on the vegetative and floral organs of all.

We may designate the different types of trichomes found in North American species of *Saurauia* as follows:

A. Unbranched hairs
- a. Unicellular
  1. Filiform—Filiform hairs consist of a single thin-walled cell. The longer ones become very flexuous (Fig. 1D).
- b. Multicellular (both longitudinally and laterally)
  2. Setose—The bristly setose hairs arise perpendicular to the epidermis. Tapering from a stout base, the weak ends of the longer setae are often bent over or broken in herbarium specimens, perhaps a result of pressing. On leaf surfaces where these trichomes occur, they range in size from mere bumps or warts to setae 2-3 mm long (Fig. 1B).
  3. Hirsute—More slender than setose hairs, hirsute trichomes also arise more or less perpendicular to the epidermis, but, are less erect and somewhat flexuous.
  4. Paleaceous—Even longer than hirsute trichomes, paleaceous indument is flattened toward the broad base, becoming circular in cross section toward the apex.
  5. Strigose—Strigose hairs bend abruptly at the swollen base. The ends of these harsh trichomes are more or less appressed to the epidermis and usually directed toward the apex of the organ on which they occur (Fig. 1A).
  6. Sericeous—Sericeous trichomes differ from the hirsute only in the fact that they lie more or less appressed to the surface. These, too, sometimes exceed 3 mm in length.
  7. Loriform—The long flexuous tip of the loriform hair, which often becomes entangled with the ends of neighboring hairs, is the only feature which distinguishes it from the sericeous hair (Fig. 1C).

B. Branched hairs
- c. Stellate and similar types
  8. Stellate—Stellate hairs are sessile; the arms are slender, radiating in the form of a star (Fig. 1F).

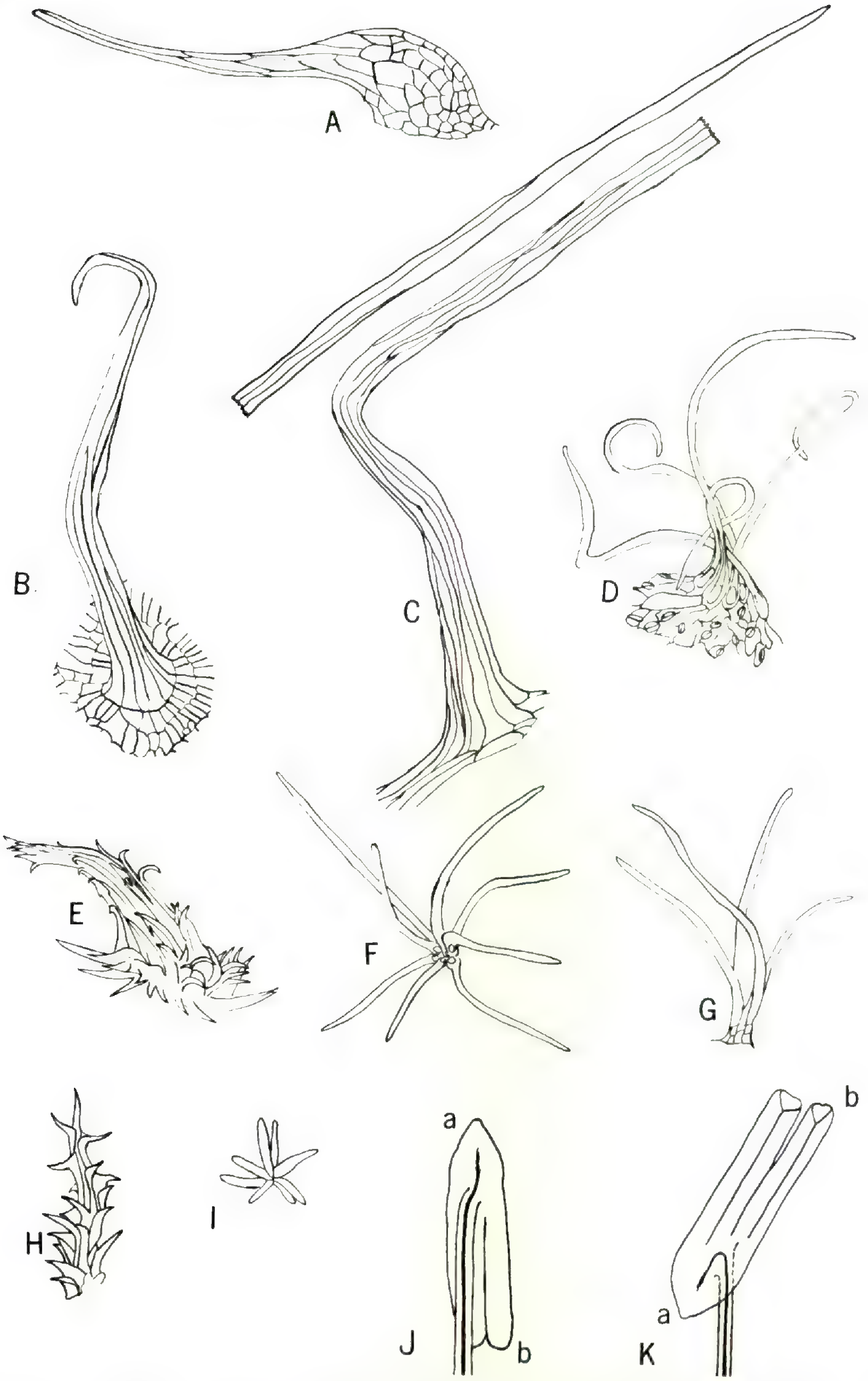


Fig. 1. Trichome types and stamens of *Saurauia*. A-D. Unbranched trichome types. A. Strigose hair on the secondary veins of the underside of the leaves, *Pringle 8201* (*S. leucocarpa*); B. Setose hair between the veins of the upperside of the leaves, *Pfeifer 1419* (*S. selerorum*); C. Loriform hair between the veins of the lower surface of the leaves, *Pfeifer 1419* (*S. selerorum*); D. Filiform hair in the axils of secondary veins of the lower surface of the leaves, *Bunting 361* (*S. serrata*). E-I. Branched trichome types. E. Tufted hairs of the secondary veins of the lower surface of leaves, *Mexia 9051* (*S. pringlei*); F. Stellate hair in the axils of the secondary veins of the lower surface of leaves, *Matuda 1198* (*S. leucocarpa*); G. Dendroid hair between the veins of the lower surface of leaves, *Allen 4663* (*S. veraguasensis*); H. Shaggy hair on the secondary veins of the lower surface of leaves, *Hunter 125* (*S. scabrida*); I. Radiate hair between the veins of the lower surface of leaves, *Allen 4671* (*S. rubiformis*). J-K. Stamen, adaxial view, showing vasculature (diagrammatic). J. In bud: a, apex of anther; b, base of anther. K. At anthesis: a, apex of anther; b, base of anther.

9. Radiate—Radiate hairs have sessile, frequently ovoid arms, less than 5 times longer than broad (Fig. 1I).
10. Dendroid—The typical dendroid hair has a single multicellular stem; the unicellular flexuous branches radiate from the apex (Fig. 1G).

d. Clustered

11. Clustered—Clustered hairs are sessile sheaf-like aggregations of cells which appear mound-shaped in surface view.

e. Shaggy

12. Shaggy—The cells which make up the single stem of the shaggy hair are coherent for part of their length, but reflexed toward their apices, giving the trichome a branched appearance throughout its entire length (Fig. 1H).

f. Tufted

13. Tufted—Tufted hairs are aggregations of cells, loosely coherent in the shape of an unbranched multicellular trichome. The loose ends of the outer cells are often directed away from the axis of the hair (Fig. 1E).

C. Scales

g. Fimbriate scales

14. Fimbriate scales—Fimbriate scales have a thickened peltate body, with hyaline fimbriae, much longer than the body, confined to one edge and aligned in a single direction (Fig. 3H).

Often, in the axils of the secondary veins on the lower surface of some leaves, filiform and stellate types of indument become entangled in a mass or tuft of hairs. If the mass is thick and more or less wadded in appearance this condition is referred to as "cottony" without distinguishing the types of hairs involved. If the mass or tuft is merely tangled without appearing wadded, the condition is referred to as "villous." In all other cases, when describing the pubescence, the structural name of the trichome is used. The diminutive denotes trichomes of a shorter length—about 1 mm or less in unbranched multicellular types.

Frequently the tip of the cells of the surface layer of multicellular unbranched trichomes are reflexed, giving the hair a shaggy appearance. The prefix "shaggy," as in "shaggy-strigose," is used to indicate this condition. If the shagginess is confined to the base of the hair it is ignored.

The density of trichomes is qualified in the keys and descriptions as follows: "Densely" indicates that the trichomes are crowded, with little or no epidermis visible between them. "Abundantly" is used when the bases of hairs are separated by about half the length of individual hairs. "Sparingly" specifies that the bases are separated by about one to five times their length. "Scattered" trichomes are usually separated by many times their length and may occur at rather regular intervals. The lack of a modifier merely indicates that the trichomes named are present. The latter designation is useful when describing heterotrichous surfaces and surfaces on which trichomes are quite scattered.

The foliar trichomes are extremely variable. Stellate and dendroid types intergrade on the same leaf. Paleaceous indument is usually found with associated hirsute trichomes and intermediate types on the same blade. Loriform emergences on the lower surface of the leaves of Honduran populations of *S. selerorum* are replaced by sericeous hairs in other populations of the same species. Often the difference between two kinds of emergences appears to be merely a matter of vigor.

The foliar indument of some species, notably *S. zahlbruckneri*, *S. conzattii* and *S. pringlei*, is more or less deciduous. The absciss scars of the indument of *S. zahlbruckneri* are completely obscured by a heavy layer of cuticle, and the upper surface of older leaves appears glabrous.

No branched hairs, other than the tufted variety, and no unicellular hairs are found on the upper leaf lamina. Vestiture of this surface is usually more dense along the veins.

Stamens: The dehiscence of the anthers of *Saurauia* has been reported as either apical or basal. The two interpretations are a result of the peculiar reorientation of the anthers at anthesis. The end of the anther which is directed toward the base of the flower in the bud becomes directed away from the base as the flower opens, rotating 180° on the filament.

The course of the trace in stamens of *Saurauia* has been followed in serial sections and in cleared and stained whole mounts. As illustrated, before anthesis (Fig. 1J), the trace is continuous toward the embryonic apex of the anther. At anthesis (Fig. 1K), the trace becomes recurved in the reorientation of the anther. This is the reverse of what would be expected if the reorientation was merely a result of inflexion. The anther is interpreted as inverted at anthesis and the embryonic base of the anther must be interpreted as the morphological base. To be precise, one must speak of the dehiscence of the anthers as basal and extrorse by rimiform pores.

The versatile anthers fork in most cases about two-thirds the distance from the base. The point of attachment of the filament is at the junction of the two thecae of the anther. The anther occasionally becomes obcordate in the smaller-flowered species.

The degree of longitudinal dehiscence of the anthers has been held by some to be useful in delimiting species. I have found, to the contrary, that the dehiscence varies considerably from flower to flower in the same inflorescence and is probably dependent upon maturation.

Stamen number is relatively constant in some species, especially those with fewer stamens, and has been used as an aid in identifying specimens.

Pollen: Twenty samples of pollen from 15 species of Mexican and Central American *Saurauia* were examined from collections at the Missouri Botanical Garden and U.S. National Herbaria. Fifteen of the specimens examined had tricolporate pollen with no discernable surface ornamentation. Five of the specimens had much larger grains which were irregularly roughened. The irregularly roughened cells are not taxonomically significant, however, since two of the species in which they occur are also among the 15 specimens with tricolporate pollen. Erdtman (1952) found two different types of grains in the South American *S. brachybotrys*. The tricolporate type was found in Steinbach's Bolivian collection, *9513*. The others, which he describes as "larger more or less irregular grains," from Steinbach's Bolivian collection (*8920*), are probably the same types as those found in my investigations. These irregularly roughened cells may represent a developmental phase of the pollen, possibly the pollen mother cells, or they may be the final phase of an abortive pollen.

No attempt has yet been made to compare critically the size of the pollen from different species. There are, however, no obvious size or structural differences.

Pistil: The ovary of Mexican and Central American species of *Saurauia* usually consists of 5 carpels. *Saurauia laevigata* is the only species which is normally 4-carpellate. The number of locules of the ovaries of *S. leucocarpa* flowers may vary from 3 to 5 in the same inflorescence. Placentation is axile, the placentas bearing numerous anatropous ovules with a single integument. Schnarf (1924) considers the hanging or descending placenta a significant departure from the ascending orientation of the ovules in most dilleniaceous genera.

The styles are filiform and free, each surmounted by a simple to capitate stigma. Some species frequently have flowers in which the pistils are aborted. Such flowers have been interpreted as unisexual, but this condition may be merely a matter of maturation. Brown (1935) has observed in the flowering pattern of *S. subspinosa,* an Asian species, that the ovary development lags behind the development of the anthers by about five days. Perhaps the small ovary lacking elongated styles may be a young stage in the ontogeny of the pistil which enlarges after the fall of the petals and the stamens.

The globose ovary is sulcate along the septa between the locules. It varies little in shape within the genus, but it does vary in size with the size of the flowers.

Saurauia veraguasensis, S. squamifructa and *S. waldheimia* have pubescent ovaries. The ovaries of the remaining species are glabrous. The wooly pubescence of the ovaries of the first two species is conspicuous at any stage of development; the vestiture of the ovaries of *S. waldheimia,* on the other hand, is often difficult to detect until the fruit has matured.

Fruit: The fruit of *Saurauia* is a berry filled with many small seeds embedded in a mucilaginous pulp. Although the size and vestiture of the fruit does vary from species to species, its characters are difficult to establish for taxonomic use since most specimens of *Saurauia* lack fruit. The seeds are areolate, about 1 mm long and about 0.5 mm wide. The testa is thin and fragile. The embryo is straight, extending about a third to a half the length of the seed and is embedded in endosperm.

Geography and Paleobotany

Saurauia species are found in the tropics of Asia and America. The number of species in Asia are more numerous (170) than in America (65). A similar disjunct distribution is known for many other genera of flowering plants and some authors have postulated a prior continuous distribution during the tertiary across a land bridge in the Bering Strait region. Paleobotanical evidence is inconclusive with regard to *Saurauia.* An impression of a *Saurauia* leaf was reported by Hollick (1936) in *The Tertiary Floras of Alaska.* His determination of the *Saurauia* specimen was apparently made from comparison with another paleobotanical specimen and not from comparison with collections of extant species of the genus. The photo of the specimen did not compare well with any *Saurauia* with which I am familiar. The tertiary veins which appear prominent in the photograph are perpendicular to the midrib of the leaf and the apex of the leaf is rounded. All species

of *Saurauia* which I have studied have leaves which are normally acute or acuminate at the apex. Five of the 22 Mexican and Central American species of *Saurauia* have leaves with the tertiary veins perpendicular to the midrib, but the veins are not prominent. I would hesitate to make a determination on the strength of a photograph and a description, but it seems very unlikely that the specimen in question represents a *Saurauia*.

Although paleobotanical evidence is inconclusive, it is quite possible that *Saurauia* may have lived in Europe during the tertiary. Hollick's citation of reported *Saurauia* impressions from Croatia raises great doubt as to the correct reference of this collection to *Saurauia*. On the other hand, the photograph (Langeron, 1900) of a collection from the tertiary of Sezanne, France, determined as *Saurauia roborans* Lang., is reminiscent of *S. tristyla* DC. as Langeron indicated in his discussion. Chandler's (1925) collection of seeds of *Actinidia* from the Eocene clays of Britain may well be *Saurauia* seeds instead; there is little difference between seeds of the two genera.

All of Gilg's (1893) taxonomic sections of *Saurauia* are known in the Old World. Only his sect. *Pleianthae*, is known in the New World. The greater speciation of tropical Asian *Saurauia* and the fact that the closely allied *Actinidia* is confined to that region suggest that the center of origin of *Saurauia* lies in the Old World. No species of *Saurauia* is known from the Antilles. Furthermore, the populations of North American *Saurauia*, for the most part, are confined to more or less contiguous mountain systems isolated from one another by lowland barriers. Smith (1941) notes a similar distribution for Papuasian *Saurauia*.

There are three centers of concentration for Mexican and Central American *Saurauia* isolated from one another by lowland barriers. One, in Mexico, is limited in the north by frosts which occasionally penetrate south of the Tropic of Cancer and by the dry climate of the central Mexican highlands. To the south, this region is bounded by the Isthmus of Tehuantepec. A second region, including Chiapas, Guatemala, British Honduras, Honduras, El Salvador and Nicaragua, is bounded on the northwest by the Isthmus of Tehuantepec and on the southeast by Lago Nicaragua and the Rio San Juan valley. The third region, including Costa Rica and Panama, is bounded on the northwest by Lago Nicaragua and the Rio San Juan valley and on the southeast by the Isthmus of Panama. South American populations of *Saurauia*, except the lowland *S. laevigata*, are effectively isolated from the Mexican and Central American ones by the broadest of its lowland barriers, the Isthmus of Panama.

Only three species seem to have a more or less continuous distribution across the lowland barriers. *Saurauia laevigata* occurs in all three regions and spreads across the Isthmus of Panama into South America. *Saurauia aspera* is found from Oaxaca in region 1 to northeast Nicaragua in region 2. *Saurauia scabrida* is found in region 1 to east central Mexico and in region 2 into Honduras.

Region 2 with its rugged topography boasts the largest number of species, 18. Region 1 with a larger area but less rugged terrain and larger mountain systems has 10 species. Region 3 with less area and a more or less continuous chain of mountains has only 5 known species.

Systematic Position

Systematists have generally referred *Saurauia* either to the *Guttiferales* or to the *Ericales*. Many have considered *Saurauia* transitional between the two. The two orders share with *Saurauia* a woody habit, axile placentation and regular, generally bisexual, frequently pentamerous flowers. If Corner's (1946) hypothesis that obdiplostemony has arisen from centrifugally developing androecia is correct, we find additional support for a relationship between the two orders through *Saurauia*. Furthermore, Erdtman (1952) has pointed out the similarities between the pollen of these groups.

Saurauia has many characters which identify it with the *Ericales*. It seems unnecessary to call attention to similarities in floral organization—superior ovary, epipetalous stamens with poricidal dehiscence of the anthers, frequent pentamery in the calyx and corolla lobes and axile placentas bearing numerous small anatropous ovules. Tetradinous pollen, frequent in the *Ericaceae*, is known for at least one species of *Saurauia* (Erdtman, 1952). An early ontogenetic inversion of the anthers occurs in *Erica* (Matthews & Taylor, 1927), similar to the late ontogenetic inversion of those of *Saurauia*. Multicellular trichomes similar to those found in *Saurauia* are frequent in ericaceous plants. Multilacunar nodal anatomy is known for both. Finally, each group is characteristically woody in habit and prefers mountainous habitats in the tropics.

It is my opinion that *Saurauia*, with its close allies *Actinidia* and *Clematoclethra*, should be referred to the *Clethraceae*. Flowers of both *Saurauia* and *Clethra* most frequently have five sepals and five basally fused petals; the aestivation of the sepals is quincuncial. The stamen number in *Saurauia* is sometimes reduced to 13 thus approaching the 10-staminate condition of *Clethra*. The tricarpellate pistil of *Clethra* corresponds to that of some Asian species of *Saurauia* and there is a tendency toward the fusion of the styles in Asian *Saurauia* which is nearly complete in many species of *Clethra*. An inversion of the anthers at anthesis, similar to that found in *Saurauia*, has been verified for *Clethra* by Thomas (1961). Similarities in the ontogeny and morphology of the ovules of *Saurauia*, *Actinidia*, *Clematoclethra* and *Clethra* were described by Lechner (1915) and Schnarf (1924). Finally, *Saurauia* shares with *Clethra* the following: unilacunar nodal anatomy, axile placentation, tricolporate unornamented pollen, numerous small seeds with straight embryos embedded in endosperm, a woody habit, mountainous tropical habitat and epipetalous stamens.

Acknowledgments

I am grateful to the curators of the following herbaria for providing the specimens used in this study: A (Arnold Arboretum, Harvard University, Cambridge), BR (Jardin Botanique de l'État, Bruxelles), F (Chicago Natural History Museum), GH (Gray Herbarium, Harvard University, Cambridge), HAL (Botanische Anstalten der Martin-Luther-Universität, Halle-Wittenberg, Germany), K (Royal Botanic Gardens, Kew, England), MICH (Herbarium, University of Michigan, Ann Arbor), MO (Missouri Botanical Garden Herbarium, St. Louis), NY (New York Botanical Garden, New York), P (Muséum National d'Histoire Naturelle, Paris), US (U.S. National Museum, Smithsonian Institution, Washington).

The administration and trustees of the Missouri Botanical Garden generously made available the facilities of the herbarium and the library where the work was carried out.

Dr. George Van Schaack of that institution was especially helpful in the use of the library. I am deeply indebted to the late Dr. Robert E. Woodson, Jr. for his suggestion and supervision of the study, and for his painstaking criticism of the manuscript. Finally, I wish to express my gratitude to my wife, Gene Anne, for her invaluable help in the preparation of the manuscript.

Systematic Treatment*

Saurauia Willd., Ges. Naturf. Fr. (Berlin) Neue Schr. **3:** 407, 1801. (Type: *S. excelsa* Willd.)

Scapha Noronha, Verh. Batav. Genoots. 5, ed. 1, Art. **4:** 3, 1770, nom. nud.
Palaua Ruiz & Pav., Fl. Peruv. Chil. Prodr. 100, 1794, non Cav. (1785). (Type: *P. lanceolata* Ruiz & Pav.)
Apetelia DC., Mém. Soc. Phys. Genève **1:** 426, 1821. (Based on *Palaua* Ruiz & Pav.)
Leucothea Moc. & Sessé ex DC., loc. cit. 419, nom. nud. pro syn.
Vanalphimia Lech. ex DC., loc. cit. 421, nom. nud. pro syn.
Marumia Reinw. ex Blume, Cat. Gew. Buitenz. 79, 1823. (Type: *M. cauliflora* Reinw. ex Blume)
Davya Moc. & Sessé ex DC., Prodr. **1:** 525, 1824, nom. nud. pro syn.
Reinwardtia Blume ex Nees, Syll. Ratisb. **1:** 96, 1824, non Dum. (1822). (Type: *R. javanica* Blume ex Nees)
Tonshia Buch.-Ham. ex D. Don, Prodr. Fl. Nep. 225, 1825. (Type: *T. polypetala* Buch.-Ham. ex D. Don)
Blumia Spreng. in L., Syst. Veg., ed. 16, **3:** 126, 1826. (Based on *Reinwardtia* Blume)
Overstratia Deschamps, Benn. Pl. Jav. Rar. 171, 1840, nom. nud.
Obelanthera Turcz., Bull. Soc. Nat. Moscou **20,** Partie 1: 148, 1847. (Type: *O. melastomacea* Turcz.)
Draytonia A. Gray, U. S. Expl. Exped. 1838-42 (Wilkes) **15:** 206, *t. 15,* 1854. (Type: *D. rubicunda* A. Gray)
Synarrhena F. Muell., Fragm. **5:** 175, 1866, nom. nud. pro syn.
Trematanthera F. Muell., Vict. Natural. **3:** 71, 1886. (Type: *T. dufaurii* F. Muell.)

Pubescent trees and shrubs. *Leaves* simple, spiral, petiolate, penninerved, estipulate. *Inflorescences* basically thyrsiform (sometimes reduced to a single flower in Asia), axillary. *Flowers* regular, basically pentamerous (*S. laevigata* usually tetramerous), pedicellate; sepals 3-6, often 5, persistent, the outer usually somewhat smaller and more densely pubescent, aestivation quincuncial; petals 3-6, usually 5, white or pink, fused at the base, falling as a unit with the stamens; stamens indefinite, the filament adnate to the base of the corolla, filiform, pubescent at the base, the anther bifurcate, versatile, extrorse, basally dehiscent by rimiform pores; ovary globose, 3- to 6-, frequently 5-locular and sulcate, the styles as many as the locules, free (sometimes coherent in Asia), filiform, obsolete to exceeding the stamens, the stigmata simple to capitate, the ovules indefinite, anatropous, the placentation axile. *Fruit* baccate, the seeds many, small, areolate, embedded in a mucilaginous pulp, the embryo straight, one-third to half as long as the seed, endosperm copious, mealy.

According to Gilg (1893), Willdenow consistently spelled *Saurauia* with an "i" in his own herbarium, not with a "j" as in the original description. The former

* Because of space limitations an alphabetical listing of exsiccatae has not been included in this paper, but a mimeographed copy is available from the author upon request. —*Editor.*

spelling is orthographically correct as indicated in the International Code to Botanical Nomenclature of 1961 (Art. 73: note 6 and examples).

Key to the Series of Mexican and Central American Saurauia

a. Leaves with tertiary veins elevated, more prominent than the lesser reticulation (except sometimes *S. waldheimia*); plants often copiously pubescent.
  b. Sepals densely pubescent, sometimes partly glabrous within, the margins obscured by the pubescence (see also *S. seibertii*); ovary and fruit glabrous .... I Gymnogynae
  bb. Inner and imbricate sepals partly glabrous, frequently completely glabrous within, ciliate.
    c. Ovary and fruit pubescent .... II Gynotrichae
    cc. Ovary and fruit glabrous .... III Oreophilae
aa. Leaves with tertiary veins immersed, scarcely more prominent than the lesser reticulation; plants sparingly pubescent; ovary and fruit glabrous .... IV Laevigatae

Series I

Gymnogynae Busc., Malpighia **25:** 221, 1912, emend.

Veranianae Busc., loc. cit. 219, pro parte.
Villosae Busc., loc. cit. 220, pro parte minore.
Basilatae Busc., loc. cit. 221, pro parte.
Scabrae Busc., loc. cit. 224, pro parte minore.

a. Leaves chartaceous to coriaceous, pubescent above and beneath, usually wider than 6 cm, the secondary veins frequently more than 17 pairs.
  b. Leaves abundantly sericeous above, smooth to the touch; trichomes of the leaves and sepals frequently longer than 1 mm; stamens less than 25. Mexico: Vera Cruz and northern Oaxaca .... 1. *S. villosa*
  bb. Leaves sparingly pubescent above, usually scabrous; trichomes of the leaves and sepals rarely longer than 1 mm except along the major veins; stamens more than 25.
    c. Leaves abundantly to scattered stellate, clustered and tufted beneath, not wrinkled or blistered above.
      d. Inflorescence more than 70-flowered, flowers 9-13 mm in diam. Costa Rica .... 2. *S. pittieri*
      dd. Inflorescence usually less than 60-flowered, flowers 15-22 mm in diam. Guatemala, Costa Rica and Panama .... 3. *S. rubiformis*
    cc. Leaves densely stellate beneath, lacking other branched trichomes, cottony beside the major veins beneath, pubescent with multicellular unbranched hairs on the rugose to bullate upper surface. Mexico: Oaxaca and Chiapas .... 4. *S. comitis-rossei*
aa. Leaves membranaceous, pustulate, nearly glabrous above and beneath except the veins, 2-6 cm wide, the secondary veins 10-17 pairs. Mexico: Chiapas ..5. *S. pustulata*

1. Saurauia villosa DC., Mém. Soc. Phys. Genève **1:** 420, 1822. (ex icon.)

Leucothea villosa Moc. & Sessé ex DC., loc. cit., nom. nud. pro syn.
Davya villosa Moc. & Sessé ex DC., Prodr. **1:** 525, 1824, nom. nud. pro syn.
Obelanthera melastomacea Turcz., Bull. Soc. Nat. Moscou **20,** Partie 1: 148, 1847. (Type: *Jürgensen 896*)
Saurauia obelanthera Turcz., loc. cit. **30,** Partie 1: 245, 1858. (Type: *Jürgensen 896*)
S. pseudopeduncularis Busc., Malpighia **26:** 30, 1913. (Type: *Jürgensen 896*)
S. villosa DC. var. *hahni* Busc., loc. cit. 305. (Type: *Hahn s.n.*)
S. speluncicola Schultes, Bot. Mus. Leafl. Harvard Univ. **8:** 193, 1940. (Type: *Schultes 795*)

Shrubs to 2 m; copiously pubescent. *Leaf* blades obovate, acute to acuminate, the base acute to obtuse, frequently oblique, the margins setaceo-serrulate, 15-21

cm long, 4-13 cm wide, chartaceous, the secondary veins 15-21 pairs, the tertiary veins elevated, more prominent than the lesser reticulation, pustulate, abundantly sericeous with trichomes frequently longer than 1 mm between the veins above, usually abundantly dendroid to stellate between the veins beneath; petioles 1-7 cm long, 1-4 mm in diam. *Inflorescences* 7- to 62-flowered, 7-22 cm long, 1- 7 cm wide, the primary peduncle 3-15 cm long, the bracts linear to triangular, 2-7 mm long or foliaceous, to 30 mm long. *Flowers* 15-20 mm broad, buds to 5-7 mm in diam, the pedicels to 3-10 mm long; sepals medially densely heterotrichous, laterally densely appressed-stellate, the imbricate sepal densely heterotrichous on the exterior half, densely appressed-stellate on the interior half, the outer 2 densely heterotrichous, all densely appressed-stellate within; petals 5, white, oblong to obovate, 7-9 mm long, 4-6 mm wide, obtuse to incised at the apex; stamens 20-24, the anther 2.0-3.0 mm long, the filament 2.0-3.0 mm long; ovary 5-locular, globose, 5-sulcate, glabrous, the styles 5, obsolete to 3 mm, the stigmas simple to sub-capitate. *Berries* to 7 mm in diam, globose, 5-sulcate, glabrous.

Damp forests, hillsides, thickets, along brooks, limestone cliffs with water continually dripping on plants, temperate mountain regions; 900-1000 m; flowering from May to September.

Vernacular names: *Pipicho, Mameyito* (Oaxaco—Schultes).

MEXICO: OAXACA: Cuicatlán, *Conzatti 2498* (F); San Antonio Eloxochitlán, *Schultes & Reko 235* (GH); *Schultes 795* (GH); Sierra San Pedro Nolasco, Talea de Castro [Dist. Villa Alta], *Jürgensen 896* (K); Yotao, *Galeotti 7057* (F). VERA CRUZ: Jalapa, *Schiede & Deppe 328* (HAL); Misantla, *Hahn s.n.* (F, P); Orizaba, *Botteri 1126* (A, F, GH, MO); nr Orizaba, *Bourgeau 3041* (P), *Mohr s.n.* (US), *s.n.* (US); Zacualpan, *Purpus 1958* (F, GH, MO, US), *8005* (A), *8521* (A), *10765* (A, MO, US).

The Jürgensen collection differs from the others by lacking the rather dense stellate pilosity of the lower surface of the leaf. Buscalioni (1913) treated this collection as distinct and referred all Vera Cruz collections to *S. villosa* var. *hahni*. They are treated as one population here because of their geographical propinquity and their similarities in the long unbranched multicellular pubescence of the sepals and the upper surface of the leaves.

2. SAURAUIA PITTIERI Donn. Sm., Bot. Gaz. **23:** 237, 1897. (Type: *Pittier 10163*)

S. pseudopittieri Busc. f. *veranii* Busc., Malpighia **30:** 98, 1927. (Type: *Pittier 13205*, Donn. Sm. Pl. Guat. 7523)
S. pittieri f. *veranii* Busc., loc. cit. 210. (Type: *Tonduz 12431*, Donn. Sm. Pl. Guat. 7372)

Shrubs and trees to 8 m; copiously pubescent. *Leaf* blades obovate to elliptic, acuminate to acute, rarely obtuse, the base acute to obtuse, sometimes oblique, the margins serrulate, 18-31 cm long, 10-15 cm wide, chartaceous, the secondary veins 21-27 pairs, the tertiary veins elevated, more prominent than the lesser reticulation, scabrous with trichomes usually shorter than 1 mm between the veins above, abundantly to sparingly clustered and tufted between the veins beneath; petioles 1-5 cm long, 3-4 mm in diam. *Inflorescences* 75- to 430-flowered, 20-45 cm long, 6-15 cm wide, the primary peduncle 12-22 cm long, the bracts linear to linear-triangular, 2-15 mm long. *Flowers* 9-13 mm broad, buds to 5 mm in diam, the

pedicels 1-11 mm long; sepals 5, sometimes 4, 4-6 mm long, 3-4 mm wide, the pubescence shorter than 1 mm, the inner 2 medially densely heterotrichous, laterally densely clustered-pubescent, the imbricate sepal densely heterotrichous on the exterior half, densely clustered-pubescent on the interior half, the outer 2 densely heterotrichous, all densely clustered within; petals 5, sometimes 4, oblong to elliptic, white, 5-6 mm long, ca 2-3 mm wide, obtuse to emarginate; stamens 28-30, the anther 2.0-3.0 mm long, the filament 2 mm long; ovary usually 5-locular, globose, usually 5-sulcate, glabrous, the styles usually 5, obsolete, the stigmas simple. Mature berries not seen.

North slope, along road, forest, edge of forest; 1500-1750 m; flowering from June to September.

Costa Rica: cartago: S of Cartago, *Chrysler 5441* (F); V. Turrialba, *Pittier 13205*, Donn. Sm. Pl. Guat. 7523 (GH, US); Vara Blanca, *Skutch 3307* (MO, US). san josé: La Palma, *Pittier 10163* (NY, US); route de La Palma, *Tonduz 12431*, Donn. Sm. Pl. Guat. 7372 (GH, NY, US).

Saurauia pittieri intergrades morphologically with *S. laevigata* in Costa Rica. Specimens intermediate between the two prompted Buscalioni (1927) to recognize a third species, which he called *S. pseudopittieri.* By restudying the material annotated by him, I have been able to recognize other intermediate specimens. *Pittier 13205* with leaves like *S. laevigata* and flowers like *S. pittieri* is cited under the latter. *Tonduz 11452* with foliar pubescence intermediate between the two and flowers like the former is cited under *S. laevigata.* The disposition is made primarily on the basis of whether the flowers are 4-or 5-merous.

3. Saurauia rubiformis Vatke, Linnaea **40:** 221, 1876. (Type: *Hoffmann 814*)

S. sarapiquensis Carr., Rev. Hort. (Paris) **49:** 60, 1877. (ex char.)
S. polyantha Gilg in Engler & Prantl, Natürl. Pflanzenfam. III. **6:** 128, *fig.* 67, 1893. (ex icon.)
S. rubiformis f. *veranii* Busc., Malpighia **27:** 144, 1916. (Type: *Pittier 312*)
S. rubiformis f. *aspera* Busc., loc. cit. 145. (Type: *Tonduz 12422*, Donn. Sm. Pl. Guat. 7373)
S. pseudorubiformis Busc., loc. cit. 149. (Type: *Pittier 13202*, Donn. Sm. Pl. Guat. 7524)
S. pseudorubiformis var. *guatemalensis* Busc., loc. cit. 155. (Type: *Türckheim II778*, Donn. Sm. Pl. Guat. 8498)

Shrubs and multiple-trunked trees to 15 m; copiously pubescent. *Leaf* blades broadly to narrowly obovate to elliptic, shortly acuminate to acute, rarely obtuse, the base obtuse, rarely acute or cordate, the margins serrulate, 13-30 cm long, 5-16 cm wide, chartaceous to subcoriaceous, rarely membranaceous, the secondary veins 15-25 pairs, the tertiary veins elevated, more prominent than the lesser reticulation, scabrous with trichomes usually shorter than 1 mm between the veins above, sparingly to abundantly tufted-, clustered- or stellate-pubescent between the veins beneath; petioles ca 1.5-7.0 cm long, 2-4 mm in diam. *Inflorescences* 15 to 55-, rarely 190-flowered, 15-25, rarely to 33 cm long, 4-10, rarely to 18 cm wide, the primary peduncle 5-16 cm long, the bracts linear, triangular to foliaceous, 2-30 mm long. *Flowers* 15-30 mm broad, buds to 5-8 mm in diam, the pedicels 3-25 mm long; sepals 5, 4-8 mm long, 4-6 mm wide, the pubescence usually shorter

than 1 mm, the inner 2 medially densely heterotrichous, laterally densely clustered, the imbricate sepal densely heterotrichous on the exterior half, densely clustered on the interior half, the outer 2 densely heterotrichous, all densely clustered within; petals 5, white, oblong, 6-12 mm long, 3-7 mm wide, obtuse to incised at the apex; stamens 26-41, the anther 2-3 mm long, the filament 2-3 mm long; ovary 5-locular, globose, 5-sulcate, glabrous, the styles 5, obsolete to 4 mm, the stigmas simple. Mature fruit not seen.

Humid forests, second growth tropical rain forest, near streams; 1550-2600 m; flowering throughout the year.

GUATEMALA: ALTA VERAPAZ: region of Chelac, *Standley 70369* (F); Chicoyonity, *Smith 1719* (US); Cobán, *Türckheim II778*, Donn. Sm. Pl. Guat. 8498 (F, NY, US); region of Cocolá, *Standley 70291* (F); Pansamalá *Türckheim 990* (GH, NY, US); Senahú, *Hatch & Wilson 197* (F). QUICHÉ: Nebaj, *Skutch 1774* (A).

COSTA RICA: ALAJUELA: Topesco, *Smith 2680* (F). CARTAGO: Oapellades, *León 541* (F); V. Poas, *Pittier 312* (US), *Tonduz 10845* (US); V. Turrialba, *Pittier 13202*, Donn. Sm. Pl. Guat. 7524 (GH, US); along cart-road from Vara Blanca, *Maxon & Harvey 8470* (US); Vara Blanca de Sarapiquí, *Skutch 3504* (A, MO, US); Santa Cruz, *Holm & Iltis 123* (F, MO); Zarcero, *Smith A295* (F, MO), *A707* (F, MO). SAN JOSÉ: Las Nubes, *Valerio 1452* (F); La Palma, *Tonduz 12422*, Donn. Sm. Pl. Guat. 7373 (F, GH, NY, US); Potreros, *Dodge & Thomas 4950* (GH, MO, US); Vara Blanca, *Chrysler 5123* (F). WITHOUT PRECISE LOCALITY: Candelaria, *Hoffmann 814* (US); Térraba, *León 1101* (US); Zapote de S. Carlos, *Smith H550* (F, MO).

PANAMA: CHIRIQUÍ: Casita Alta, *Woodson et al. 957* (MO); nr Cerro Punta, *Stern & Chambers 84* (US); Chiriquí, *Allen 4797* (MO); Quebrada Velo, *Allen 4671* (F, MO), *Woodson & Schery 263* (MO, US).

This species, *S. pittieri* and *S. seibertii* are closely allied. They are similar in the distribution of the pubescence of the sepals and in the kinds of trichomes, including clustered and tufted types, making up the pubescence of both sepals and leaves. *Saurauia rubiformis* may be distinguished from *S. pittieri* by its larger flowers and from *S. seibertii* by its larger, more densely pubescent leaves.

4. SAURAUIA COMITIS-ROSSEI Schultes, Bot. Mus. Leafl. Harvard Univ. **16:** 112, 1953. (Type: *Reko 6183*)

Trees to 5 m; copiously pubescent. *Leaf* blades narrowly elliptic to obovate, acute, the base obtuse to acute, frequently oblique, the margins setaceo-serrulate, 13-31 cm long, 4-11 cm wide, chartaceous to subcoriaceous, the secondary veins 20-23 pairs, the tertiary veins elevated, more prominent than the lesser reticulation, abundantly pubescent with multicellular unbranched hairs on the rugose to bullate surface between the veins above, densely dendroid and stellate between and cottony bordering the veins beneath; petioles 3-4 cm long, 2-4 mm in diam. *Inflorescences* 33- to 44-flowered, 10-15 cm long, 3-8 cm wide, the primary peduncle 5-10 cm long, the bracts linear to triangular, 1-10 mm long. *Flowers* 15 mm broad, buds to 4-5 mm in diam, the pedicels to 3-15 mm wide, the inner 2 medially densely heterotrichous, laterally densely radiate, the imbricate sepal densely heterotrichous on the exterior half, densely radiate on the interior half, the outer 2 densely heterotrichous, all submarginally radiate within; petals 5, sometimes 6, white, 6-8 mm long, 3-4 mm wide, obtuse to incised at the apex; stamens 31-40, the anther 2 mm long, the filament 3 mm long; ovary 5-locular, globose, 5-sulcate, glabrous, the

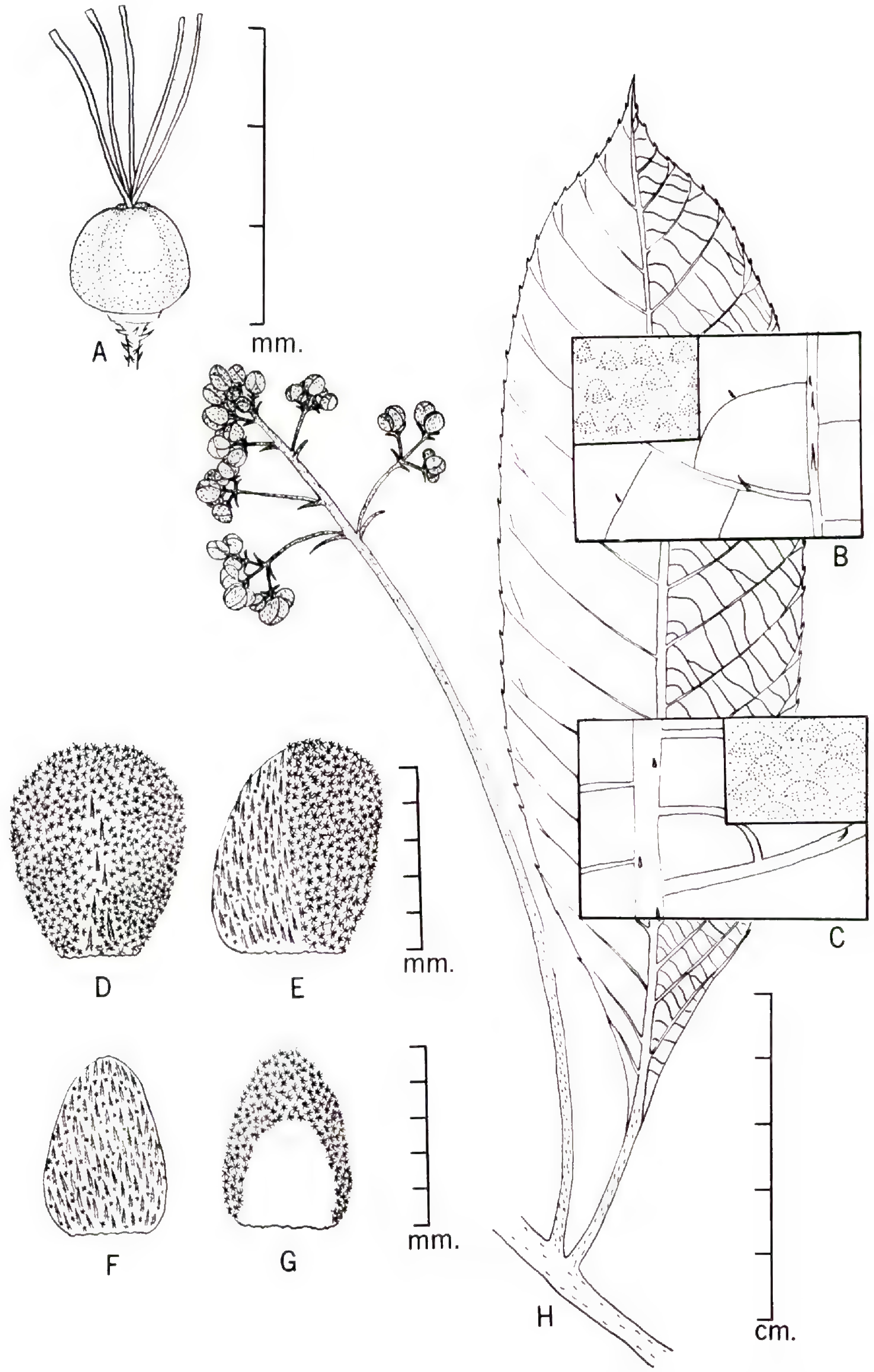


Fig. 2. *S. pustulata.* A. Ovary; B. Upper leaf surface (inset—pustulate epidermis); C. Lower leaf surface (inset—pustulate epidermis); D. Inner sepal, outer surface; E. Imbricate sepal, outer surface; F. Outer sepal, outer surface; G. Outer sepal, inner surface; H. Leaf and inflorescence.

4-5 styles obsolete to 4 mm long, the stigmas simple to subcapitate. *Berries* 5-6 mm in diam, globose, 5-sulcate, glabrous.

Open oak-pine forest; 1700-2000 m; flowering December to April.

Vernacular name: *Mameyito* (Oaxaca—Reko).

MEXICO: CHIAPAS: 10 km S of Ciudad de Las Casas, *Little & Sharp 9979* (MICH); Paraje of Koltol Té, Municipio of Tenejapa, *Breedlove 6152* (US). OAXACA: 184 km S of Oaxaca, *Carlson 2713* (F); Pochutla, *Reko 6183* (GH, NY).

The inflorescences of *S. comitis-rossei* and *S. pustulata* are invested with the same kind of pubescence. The two species are distinguished by marked differences in foliar pubescence and texture.

5. SAURAUIA **PUSTULATA** G. E. Hunter, sp. nov.

Frutices vel arbores ramulis dense strigillosis. *Foliorum* lamina anguste elliptica vel anguste obovata acuminata basi cuneata margine serrulata 8-19 cm longa 2-6 cm lata membranacea nervis secundariis 10-17 paribus nervis tertiariis quam reticulo minore prominentioribus pustulata vix strigillosa in utraque pagina; petiolus 1-2 cm longus 1-2 mm latus sparse strigillosus. *Inflorescentia* 30- vel 50-flora 8-19 cm longa 3-5 cm lata pedunculo primario 5-15 cm longo dense strigilloso atque dense radiato-piloso bractiis linearibus vel triangularibus 1-5 mm longis. *Flores* 12 mm lati pedicellis 2-4 mm longis dense hirtellis atque radiato-pilosis; sepala 5 ca 5 mm longa 3-4 mm lata extus 2 interiora medio dense strigillosa atque radiato-pilosa 1 imbricatum dimidia parte exteriore dense strigillosum atque radiato-pilosum interiore dense radiato-pilosum 2 exteriora dense strigillosa atque radiato-pilosa intus omnia submargine radiato-pilosa aliter glabra; petala 5 obovata vel oblonga 5-6 mm longa 2-3 mm lata; stamina 30 anthera 2 mm longa filamento 2 mm longo; ovarium globosum glabrum loculis 5; styli 5 liberi ca 2 mm longi stigmatibus simplicibus. *Fructus* ignotus.

Shady forest, along brook, mountains; flowering in May and June.

MEXICO: CHIAPAS: Fenia, *Purpus 10333* (NY, US, holotype); Lobani [Líbano?], *Liebmann 373* (F).

SERIES II

GYNOTRICHAE Busc., Malpighia **25:** 220, 1912, emend.

Barbigerae Busc., loc. cit. 223, pro parte minore.

a. Leaves frequently longer than 15 cm; usually stellate-pubescent beneath, the tertiary veins elevated, more prominent than the lesser reticulation, ovary and fruit densely pubescent; sepals distinctly heterotrichous without, partly glabrous without and within.
 b. Inflorescence 7- to 94-, usually more than 12-flowered; ovary densely pubescent with filiform hairs. Honduras, Costa Rica and Panama ....6. *S. veraguasensis*
 bb. Inflorescence 1- to 5-flowered; ovary densely pubescent with fimbriate scales. Honduras ....7. *S. squamifructa*

aa. Leaves rarely longer than 15 cm, pubescent only with unbranched multicellular hairs, except the villous-barbate axils of the secondary veins beneath, the tertiary veins more frequently immersed, scarcely more prominent than the lesser reticulation; sepals primarily homotrichous with unbranched multicellular hairs, partly glabrous without, glabrous within; inflorescence 1- to 11-flowered; ovary and fruit abundantly to scattered pubescent with filiform hairs (nearly glabrous in Honduras). Guatemala, Honduras and Nicaragua ....8. *S. waldheimia*

6. Saurauia veraguasensis Seem., Bot. Voy. Herald 249, 1854. (Type: *Seemann 1235*)

S. montana Seem., loc. cit. 87. (Type: *Seemann 1235*)
S. costaricensis Donn. Sm., Bot. Gaz. **23**: 236, 1897. (Type: *Cooper 304*, Donn. Sm. Pl. Guat. 5714)
S. ovalifolia Donn. Sm. loc. cit. **42**: 292, 1906. (Type: Donn. Sm. Pl. Guat. 4746)
S. pseudoscabrida Busc., Malpighia **25**: 10, 1912. (Type: Donn. Sm. Pl. Guat. 4745)
S. costaricensis var. *brachitricha* Busc., loc. cit. **27**: 12, 1915. (Type: *Tonduz 1744*)
S. costaricensis var. *dolicotricha* Busc., loc. cit. 15. (Type: *Tonduz 11690*)
S. pseudocostaricensis Busc., loc. cit. 25. (Type: Donn. Sm. Pl. Guat. 4745)
S. pseudovaraguensis Busc., loc. cit. 30. (Type: *Seemann 1235*)
S. engleriana Busc., loc. cit. 131, 1916. (Type: *Pittier 56*)
S. setosa Standl., Field Mus. Publ. Bot. **18**: 693, 1937. (Type: *Standley & Valerio 51979*)

Shrubs and trees to 15 m; copiously pubescent. *Leaf* blades narrowly elliptic to obovate, acute to acuminate, the base obtuse to acute, frequently oblique, the margins setaceo-serrulate to serrate, 11-40 cm long, 3-18 cm wide, chartaceous to subcoriaceous, the secondary veins 14-26 pairs, the tertiary veins elevated, more prominent than the lesser reticulation, sparingly to abundantly strigillose, sericeous, setulose or hirtellous between the veins above, usually stellate or dendroid between the veins beneath, the axils of the secondary veins frequently villous-barbate beneath; petioles 1-9 cm long, 2-4 mm in diam. *Inflorescences* 7- to 94-flowered, 7-30 cm long, 3-18 cm wide, the primary peduncle 4-10 cm long, the bracts foliaceous or linear to triangular, 1-50 mm long. *Flowers* 13-27 mm broad, buds to 5-8 mm in diam, the pedicels to 3-10 mm long; sepals 5, 4-7 mm long, 3-7 mm wide, the inner 2 medially densely heterotrichous, laterally appressed-stellate, submarginally glabrous, ciliate, the imbricate sepal densely heterotrichous on the exterior half, appressed-stellate, submarginally glabrous, ciliate on the interior half, the outer 2 densely heterotrichous, all submarginally appressed-stellate, glabrous elsewhere within; petals 5, white to pinkish, oblong to obovate, 7-11 mm long, 4-9 mm wide, obtuse to incised at the apex; stamens 23-48, the anther 1.5-2.5 mm long, the filament 1.5-3.0 mm long; ovary 5-locular, globose, densely pubescent with filiform trichomes, the styles 5, obsolete to 4 mm long, the stigmas simple to subcapitate. *Berries* 6-10 mm in diam, globose, densely pubescent with filiform trichomes.

Cloud forest, rain forest, open sunlight, brushy stream bank, edge of forest, pastures, open semitropical valleys, wet rocky thicket, rocky woody stream bank; 640-2300 m; flowering throughout the year.

Vernacular names: *Capulín* (Honduras—Molina); *Cerbatana, Confiti, Moco* (Honduras—von Hagen); *Moquito* (Costa Rica—Standley & Torres); *Nance* (Costa Rica—Standley).

Honduras: comayagua: above the plains of Siguatepeque, *Yuncker et al. 6263* (F, GH, MO). el paraiso: Manzaragua, *Williams & Molina 11485* (F, GH, MO). morazán: region of Agua Amarilla, above El Zamorano, *Standley et al. 5084* (F); along Quebrada El Gallo above El Jicarito, *Standley 22481* (F); region of El Jicarito, above El Zamorano, *Molina 796* (F, GH),*Standley 24216* (F); Quebrada el Horno, entre el Frijolar y Tabla Granda, *Molina 832* (F); nr Joya Grande, on road from El Zamorano to Suyapa, *Standley & Molina 4430* (F); Montaña Zanquin, *Molina 2962* (F, GH). yoro: Portillo Grande, *von Hagen & von*

Hagen 1037 (F, NY); Subirana, *von Hagen & von Hagen 1088* (F, NY), *1097* (F, NY). TEGUCIGALPA: Tegucigalpa, *von Hagen & von Hagen 1190* (F, NY).

COSTA RICA: ALAJUELA: San Ramón, *Brenes 1619a* (NY), *4060* (F, NY), *5352* (F, NY), *20477* (F, NY), *21907* (F, NY), *Tonduz 17676* (F, K, US). CARTAGO: Agua Caliente del Llano, *Brenes s.n.* (NY); Atirro, *Smith 6446* (GH, US); Cartago, *Cooper 304,* Donn. Sm. Pl. Guat. 5714 (F, GH, US); Cerro de La Carpintera, *Standley 35729* (US); Copey, *Tonduz 11690* (F, GH, NY, US), *11899* (US), *12205* (US); Dulce Nombre, *Standley 35935* (US); La Estrella, *Standley 39321* (US); El Muñeco, S of Navarro, *Standley 33547* (US), *Standley & Torres 50912* (US), *51273* (US); Navarro, *Smith 4746* (GH, US); nr Tres Ríos, *Williams 16138* (F); region of Zarcero, *Smith A398* (F, MO). HEREDIA: nr Cariblanco, *Williams 16422* (F); Cerro de las Caricias, N of San Isidro, *Standley & Valerio 51970* (F, US), *51979* (F, US), 51994 (US); Los Angeles de Heredia, *Brenes 1920* (NY); Yerba Buena, NE of San Isidro, *Standley & Valerio 49905* (US), 49935 (US). SAN JOSÉ: Alajuelita, *Smith 4745* (US); Cerro de Piedra Blanca, above Escasú, *Standley 32488* (F, US); vic of El General, *Skutch 2651* (GH, MO, US), *3814* (A, MO, US); La Hondura, *Standley 36127* (US), *36537* (US), *37598* (F, US), *Standley & Valerio 51890* (F, US); Las Nubes, *Standley 38355* (US); vic of Santa María de Dota, *Standley 41602* (US), *Standley & Valerio 44063* (US), *44069* (US), *44114* (US); ca 7 km N of Santa María de Dota, *Standley 42947* (US). WITHOUT PRECISE LOCALITY: La Cruz de Alajuelita, *Solis 386* (F, MO); Naranjo, *Oersted 359* (F), 375 (F); Montes de Oca, *Echeverria 539* (F); San Marcos, *Tonduz 7685* (US); Río Segundo, *Tonduz 1744* (US); Río Torres a San Francisco de Guadelupe, *Pittier & Tonduz 8959* (US), *Pittier 13020* (US); Turrialba, *Pittier 56* (BR); La Ventolera, S slope of the V. Poás, *Standley 34593* (US).

PANAMA: CHIRIQUÍ: Bajo Chorro, Boquete District, *Davidson 190* (A, F, MO); vic of Bajo Mona & Quebrada Chiquero, *Woodson & Schery 521* (GH, MO, US); trail from Bambito to Cerro Punta, *Allen 314* (A, F, GH, MO, US); vic of Boquete, *Allen 4650* (MO), *Bro. Maurice 698* (GH, US), *Maxon 4932* (US), *Pittier 2874* (F, US), *2942* (F, US); V. Chiriquí, Boquete District, *Davidson 979* (A, F, MO, US), *Seemann 1235* (K); Cerro Horqueta, Boquete region, *von Hagen & von Hagen 2052* (MO); vic of Monte Lirio, valley of upper Río Chiriquí Viejo, *Seibert 303* (F, MO); Río Chiriquí Viejo valley, betw El Volcán & Cerro Punta, *White 3* (F, GH, MO); valley of upper Río Chiriquí Viejo, *White 24* (MO); Río Chiriquí Viejo valley, nr El Volcán, *White 188* (MO, US); Casita Alta, V. Chiriquí, *Woodson et al. 809* (A, F, MO); vic of "New Switzerland," central valley Río Chiriquí Viejo, *Allen 1356* (GH, MO, US).

The broad range of variability manifested by the numerous collections of this species may account for the long synonymy. Specimens have most often been identified as *S. costaricensis,* probably because of J. Donnell Smith's numerous collections in Costa Rica and because Buscalioni never accepted the name *S. veraguasensis;* he published a new name, *S. pseudoveraguensis,* citing only Seemann's type collection. The most recent name, *S. setosa,* is based on plants with multicellular unbranched hairs much longer and more erect than usual. In all other respects these plants fall within the range of morphological variation of the species.

7. SAURAUIA **SQUAMIFRUCTA** G. E. Hunter, sp. nov.

Frutices vel arbores ramulis dense sericeis. *Foliorum* lamina anguste elliptica vel obovata acuminata basi cuneata margine serrulata 9-22 cm longa 3-6 cm lata chartacea nervis secundariis 15-24 paribus nervis tertiariis quam reticulo minore prominentioribus supra in parenchymate dense strigillosa setulosa nervatione dense sericeo vel strigilloso infra in parenchymate stellato-dendroideo-pilosa nervatione dense sericeo stellato-piloso ac in axillis costae villoso-barbata; petiolus ca 1-3 cm longus ca 1-2 mm latus dense sericeus vel hirsutus atque stellato-pilosus. *Inflorescentia* 1- vel 5-flora 3-9 cm longa 2-7 cm lata pedunculo primario 2-6 cm

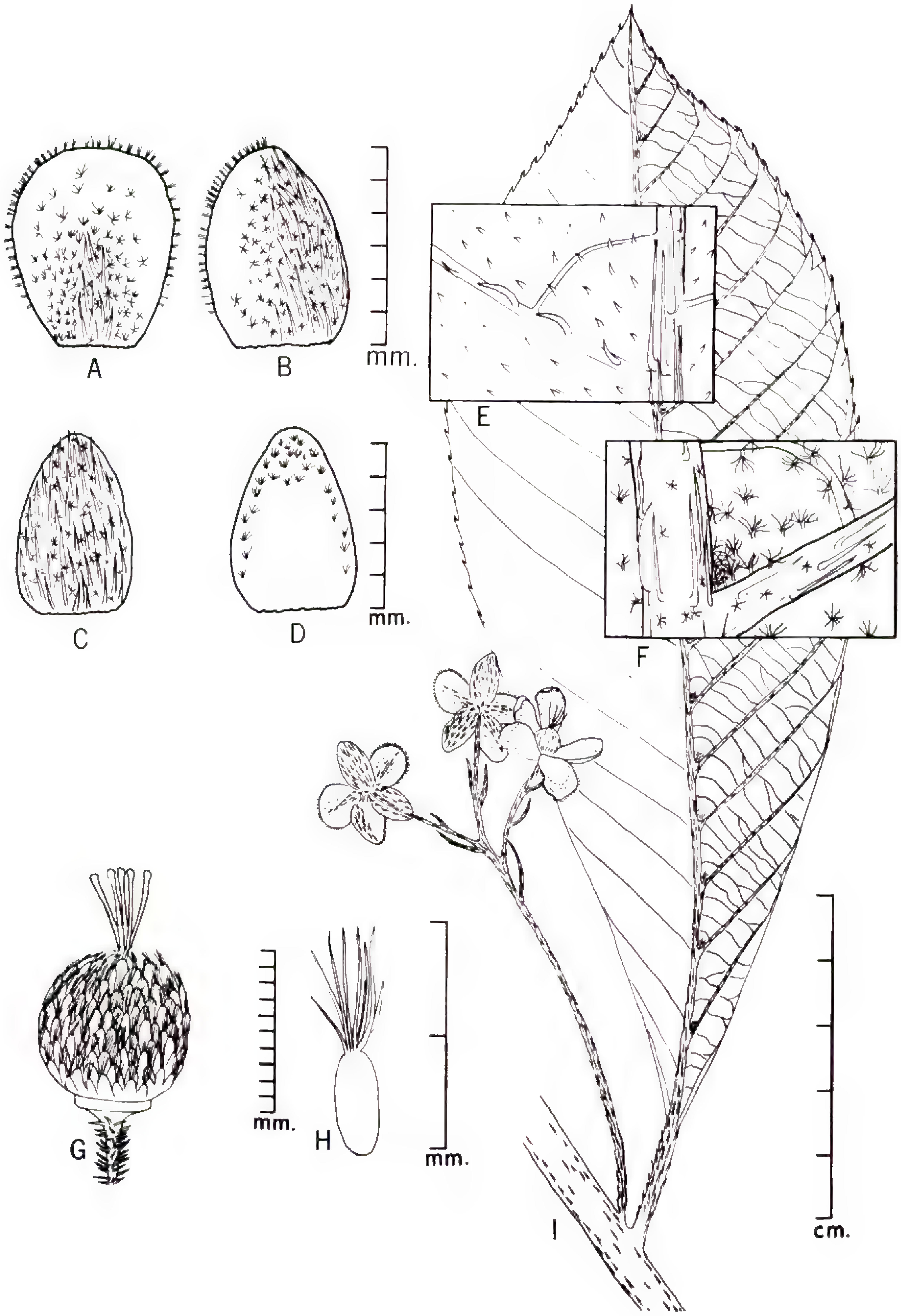


Fig. 3. *S. squamifructa.* A. Inner sepal, outer surface; B. Imbricate sepal, outer surface; C. Outer sepal, outer surface; D. Outer sepal, inner surface; E. Upper leaf surface; F. Lower leaf surface; G. Fruit; H. Fimbriate scale of the fruit; I. Leaf and inflorescence bearing young fruit.

longo dense sericeo vel hirsuto atque stellato-piloso bractiis linearibus vel lineari-triangularibus 3-15 mm longis. *Flores* ca 22 mm lati pedicellis 5-25 mm longis dense hirsutis vel hirtellis atque stellato-pilosis; sepala 5 ca 8 mm longa ca 5-6 mm lata extus 2 interiora medio dense hirtella atque stellato-pilosa submargine glabra ciliata 1 imbricatum dimidia parte exteriore dense hirtellum atque stellato-pilosum interiore stellato-pilosum submargine glabrum ciliatum 2 exteriora dense hirtella atque stellato-pilosa intus omnia submargine stellato-pilosa aliter glabra; petala 5 obovata vel oblonga ca 10 mm longa 7 mm lata; stamina 22 anthera 3.5-4.0 mm longa filamento 2.5 mm longo; ovarium globosum dense fimbriato-squamo-pilosum loculis 5; styli 5 liberi ca 4 mm longi stigmatibus capitatis. *Fructus* globosus 8-13 mm latus dense fimbriato-squamo-pilosus.

Open slopes, forest on valley floor, barranca; 1050-2000 m; flowering from November to April.

HONDURAS: COMAYAGUA: Barranco Trincheras, *Allen 6208* (F, US); *Williams & Molina 18047* (F, US); Valibrea, *Valerio 2747* (F); INTIBUCÁ: Sierra Opalaca, Pela Nariz, *Hawkes, Hjerting & Lester 2105* (F, holotype). MORAZÁN: Rosario Mone, San Juancito, *Williams 17406* (F).

8. SAURAUIA WALDHEIMIA Busc., Malpighia **28:** 488, 1920. (Type: *Rothschuh 389,* photo MO)

S. veneficorum Standl. & Steyerm., Field Mus. Publ. Bot. **23:** 217, 1947. (Type: *Steyermark 31081*)

Shrubs or small trees to 8 m, sparingly to copiously pubescent. *Leaf* blades narrowly elliptic to obovate, acuminate, rarely obtuse, the base acute, rarely obtuse, the margins serrulate, 4-17 cm long, 1-6 cm wide, membranaceous to chartaceous, the secondary veins 8-16 pairs, the tertiary veins elevated to immersed, glabrous to abundantly pubescent with only multicellular unbranched hairs between the veins above and beneath except the villous-barbate axils of the secondary veins beneath; petioles 0.5-2.0 cm long, 0.5-1.5 mm in diam, flattened to canaliculate above. *Inflorescences* 1- to 11-flowered, 3-9 cm long, 1-5 cm wide, the primary peduncle 1-5 cm long, the bracts foliaceous or linear, 2-15 mm long. *Flowers* 12-18 mm broad, buds to 4-7 mm in diam, the pedicels to 5-20 mm long; sepals 5, 4-5 mm long, 4-6 mm wide, primarily homotrichous with unbranched multicellular hairs, sometimes also appressed-stellate, the inner 2 medially densely to sparingly pubescent, laterally glabrous, ciliate, the imbricate sepal densely to sparingly pubescent on the exterior half, glabrous on the interior half, ciliate, the outer 2 densely to sparingly pubescent, sometimes also appressed-stellate, all glabrous within; petals 5, white, oblong to obovate, 7-8 mm long, 4-6 mm wide, obtuse to incised at the apex; stamens 21-24, the anther 2.0-2.5 mm long, the filament 2-3 mm long; ovary 5-locular, globose, 5-sulcate, abundantly to sparingly pubescent with filiform trichomes, the styles 5, obsolete to 2 mm, the stigmas simple to capitate. *Berries* 8-10 mm in diam, globose, 5-sulcate, abundantly to scattered filiform, nearly glabrous in Honduran plants.

Oak forest, oak-pine forest, cloud forest, moist thicket, ravine, near watercourse,

by road, upper slopes, along river; 500-2500 m; flowering from October to February.

Guatemala: chiquimula: SE of Concepción de las Minas, *Steyermark 31044* (F), *31081* (F); 3-5 mi N of Jocotán, *Steyermark 31626* (F, US). zacapa: bordering quebrada Alejandria, summit of Sierra de las Minas, *Steyermark 29913* (F); bordering Río Lima, Sierra de Las Minas, *Steyermark 30045* (F); along Río Repollal Sierra de Las Minas, *Steyermark 42526* (A, F, NY), *42547* (A, F, NY, US); upper reaches of Río Sitio Nuevo, *Steyermark 43231* (F).

El Salvador: santa ana: Cerro Montecristo, *Allen & Severen 7126* (F, NY, US).

Honduras: el paraíso: Mt Yuscarán, *Molina 621* (F). morazán: betw La Labranza & Las Flores, *Molina 1301* (F, GH, MO); along trail from Las Flores to La Labranza, *Standley 13440* (F); Mt Uyuca, *Standley & Molina 4251* (F), *Williams & Molina 11919* (F, GH, MO), *Williams & Williams 18623A* (US).

nicaragua: jinotega: Jinotega, *Grant 7300* (A, F), *7326* (A, F); nr Santa María, *Hawkes et al. 2201* (F). without precise locality: in monte Pantasma, *Oersted 360* (F).

Saurauia waldheimia is the only species that deviates significantly in the character of leaf venation on which the primary dichotomy of the key to the series is based. Specimens of two concentrations of this species, one in the Sierra de las Minas of Guatemala and the other in Nicaragua, characteristically have the tertiary veins of the leaves immersed. To the south of the Sierra de las Minas in Guatemala and extending into El Salvador, plants have leaves in which the tertiary veins are conspicuously elevated. Specimens from Honduras are intermediate in this character. Leaf size and the length and density of the multicellular unbranched hairs also are highly variable. The most dependable characters for identifying this species are the distribution of the pubescence of the sepals, the presence of filiform hairs on the ovary and the villous-barbate axils of the secondary veins on the underside of the leaves.

Series III

Oreophilae Busc., Malpighia **25:** 219, 1912, emend.

Mesophyllae Busc., loc. cit. 218, pro parte.
Villosae Busc., loc. cit. 220, pro parte.
Gymnogynae Busc., loc. cit. 221, pro parte.
Basilatae Busc., loc. cit., pro parte minore.
Barbigerae Busc., loc. cit. 223, pro parte.
Laevigatae Busc., loc. cit. 224, pro parte minore.

a. Leaves heterotrichous beneath with multicellular unbranched and stellate or filiform trichomes (sometimes only the young leaves stellate or filiform in *S. zahlbruckneri* and *S. oreophila*).

b. Leaves usually abundantly setulose, rarely tuberculate or pustulate, opaque above, densely to abundantly stellate beneath (sometimes the blades nearly glabrous in *S. oreophila*).

c. Inflorescence 35- to 200-flowered; leaves normally wider than 8 cm; sepals submarginally pubescent within; stamens 25-52. Eastern and southern Mexico to Honduras .... 9. *S. scabrida*

cc. Inflorescence usually less than 35-flowered, the leaves usually narrower than 8 cm; sepals glabrous within.

d. Sepals usually shorter and narrower than 3 mm, sparingly stellate or tufted and scattered-strigillose, the stellate trichomes more conspicuous; stamens 22-27, the anthers about 1 mm long. Mexico: Michoacan, Guerrero and Oaxaca .... 10. *S. pringlei*

dd. Sepals frequently longer and wider than 3 mm, abundantly strigose or shaggy-strigillose and less conspicuously appressed-stellate; stamens 21-24, the anthers 2-2.5 mm long. Mexico: Chiapas; Guatemala .... 11. *S. oreophila*

bb. Leaves glabrous or abundantly to sparingly sericeous above, frequently glossy above, villous or cottony in the axils of the secondary veins beneath, otherwise glabrous or abundantly to sparingly hirsute beneath; sepals glabrous within; stamens 30-35, the anthers ca 2 mm long. Mexico: Chiapas; Guatemala .... 12. *S. zahlbruckneri*

aa. Leaves homotrichous beneath with only multicellular unbranched trichomes except in the sometimes villous-barbate axils of the secondary veins (*S. selerorum* sometimes also stellate).

e. Leaves densely to abundantly pubescent above (*S. conzattii* sometimes glabrescent).

f. Leaves densely to abundantly setose-setulose above or villous-barbate in the axils of the secondary veins beneath; branch tips never paleaceous; inflorescence 30- to 175-flowered.

g. Sepals, petioles and peduncles abundantly to densely pubescent with trichomes usually shorter than 2 mm; flowers 11-14 mm broad, the inner and imbricate sepals subapically pubescent within .... 13. *S. aspera*

gg. Sepals, petioles and peduncles densely to abundantly pubescent with trichomes frequently longer than 2 mm; flowers 14-22 mm broad, the sepals glabrous within .... 14. *S. selerorum*

ff. Leaves abundantly sericeous, hirsute or glabrescent above, not barbate in the axils of the secondary veins beneath; branch tips sometimes paleaceous; inflorescence 6- to 67-flowered; sepals, petioles and peduncles densely to abundantly paleaceous or hirsute, the trichomes frequently longer than 2 mm; sepals glabrous within .... 15. *S. conzattii*

ee. Leaves scattered-pubescent above (*S. serrata* rarely abundantly minutely sericeous).

h. Sepals hoary-pubescent with minute branched trichomes, the outer and imbricate sepals subapically pubescent within; leaves villous-barbate in the axils of the secondary veins beneath; inflorescence 18- to 78-flowered. Mexico: Vera Cruz and Oaxaca .... 16. *S. pendunculata*

hh. Sepals scattered to abundantly strigillose, rarely densely hirsute to sericeous, not hoary-pubescent, the inner and imbricate sepals rarely subapically pubescent.

i. Leaves about 2.5 times longer than broad, frequently villous-barbate in the axils of the secondary veins beneath; inflorescence 12- to 56-flowered. Mexico: Sinaloa to Oaxaca .... 17. *S. serrata*

ii. Leaves about 3 times longer than broad, not barbate in the axils of the secondary veins beneath; inflorescence 4- to 20-flowered. Mexico: Chiapas; Guatemala .... 18. *S. angustifolia*

9. Saurauia scabrida Hemsl., Diagn. Pl. Nov. 3, 1878. (Type: *Bourgeau 1747*)

S. nelsoni Rose, Contr. U. S. Nat. Herb. **8:** 52, 1903. (Type: *Nelson 800*)
S. selerorum Busc., var. *pseudonelsoni* Busc., Malpighia **26:** 107, 1913. (Type: *Galeotti s.n.*)
S. villosa DC. var. *macrantha* Busc., loc. cit. 310. (Type: *Nelson 464*)
S. villosa var. *tuberculata* Busc., loc. cit. 312 (Type: *Heyde & Lux 6077*)
S. villosa var. *scabrida* Busc., loc. cit. 390, 1914. (Type: *Hahn s.n.*)
S. scabrida var. *hemsleyana* Busc., loc. cit. 409. (Type: *Bourgeau 3041*)

Shrubs and trees to 13 m; copiously pubescent. *Leaf* blades elliptic to obovate, acute to acuminate, the base acute to obtuse, frequently oblique, the margins setaceo-serrulate, 10-40 cm long, 5-19 cm wide, chartaceous to subcoriaceous, the

secondary veins 17-27 pairs, the tertiary veins elevated, more prominent than the lesser reticulation, abundantly setulose (trichomes frequently reduced to mere warts at the northern extension of this species) between the veins above, densely to abundantly stellate or dendroid between the veins beneath; petioles 1-5 cm long, 2-6 mm in diam, terete to somewhat canaliculate above near the blade. *Inflorescences* 35- to 200-flowered, 9-28 cm long, 3-13 cm wide, the primary peduncles 7-17 cm long, the bracts linear-triangular to triangular, 1-8 mm long. *Flowers* 12-15 mm broad, buds to 4-6 mm in diam, the pedicels to 3-15 mm long; sepals 5, 4 mm long, 3-4 mm wide, the inner 2 medially densely heterotrichous, submarginally glabrous, ciliate, the imbricate sepal densely heterotrichous on the exterior half, submarginally glabrous, ciliate on the interior half, the outer 2 densely heterotrichous, all submarginally radiate-pubescent within; petals 5, white to pinkish, oblong to obovate, 6-9 mm long, 3-5 mm wide, obtuse to incised at the apex; stamens 25-52, the anther 2 mm long, the filament 2 mm long, ovary 4- to 5-locular, globose, 4- to 5-sulcate, glabrous, the styles 4-5, obsolete to 4 mm long, the stigmas simple to subcapitate. *Berries* 5-6 mm in diam, globose, 4- to 5-sulcate, glabrous.

Pine woods, near river, second growth thicket, wet thicket, damp pine forest, slopes, barranca, open sun, red sandy soil, sandy hillsides, ravine, edge of mesophytic forest, liquidambar forest, along road; 500-2100 m; flowering throughout the year.

Vernacular names: *Nistamalillo* (San Luis Potosí—Edwards), *Cerbatana* (Guatemala—Steyermark), *Moco* (Guatemala—Standley).

Mexico: chiapas: Mt Ovando, *Matuda S-172* (MICH, MO); betw Teneapa & Yajalon, *Nelson 3249* (GH, US). hidalgo: Chapulhuacán, *Kenoyer 982* (F); *Lundell & Lundell 7164* (MICH, NY); S of Chapulhuacán, *Clark 7402* (MO); nr Chapulhuacán, *Hunter* 33 (MO); Cuesta grande de Chiconquiaco, *Schiede & Deppe 329* (HAL); on hwy betw Santa Ana & Chapulhuacán, *Moore 3394* (GH, US); Jacala, *Hitchcock & Stanford 6976* (GH, US). oaxaca: Hacienda de Caciques, *Smith 614* (GH); Totontepec, *Nelson 800* (US). san luis potosí: Tamazunchale, *Edwards 650* (F, MO); *Chute M-24* (MICH); nr Xilitla, *Hunter 125* (MO). vera cruz: Valle de Cordova, *Bourgeau 1747* (F, P); V. Tuxtla, *Nelson 464* (US); Misantla, *Hahn s.n.* (F); Orizaba, *Botteri 210* (F). without precise locality: Huatemalco, *Liebmann 361* (US); S. Martín, *Galeotti s.n.* (BR); Tlapacoyo, *Liebmann 362* (F); Yalala, *Liebmann 372* (F).

Guatemala: alta verapaz: betw Chirriacté & Semococh, *Steyermark 46325* (F); Cobán, *Standley 69085* (F), *69329* (F), *69420* (F); *Türckheim 30* (GH, NY, US), *II778* (F, GH, MO); 2 mi E of Cobán, *King 3316* (MICH, US); Saquijá, 43 km NE of Cobán, *Standley 70136* (F); ca 2 mi W of Santa Cruz, *King 3335* (MICH, US); Senahú, *Hatch & Wilson 151* (F). guatemala: Chinautla, *Smith 2518* (GH, US); *Hayes s.n.* (F, MO, US); Guatemala City, *Lewis 842* (F); barranca N of Guatemala City, *Popenoe 721* (A, US); "La Aurora," *Aguilar 472* (F); Las Vacas barranca, *Hayes s.n.* (F, GH). huehuetenango: pine woods of Cerro Jolomtac, Sierra de los Cuchumatanes, *Steyermark 49501* (F); Jacaltenango, *Seler & Seler 3100* (GH); Soloma, *Skutch 1061* (A). quiché: *Aguilar 1141* (F); Nebaj, *Skutch 1718* (A, F, US). santa rosa: Río de los Esclavos, *Heyde & Lux 6077* (F, GH, US). zacapa: along Rillito del V. Monos, *Steyermark 42368* (A, F).

El Salvador: chalatenanago: betw San Ignacio & Citala, *Allen 7104* (F, US).

Honduras: comayagua: nr El Achote, *Yuncker et al. 5889* (F, GH, MO, US); 10 mi NW of Siguatepéque, *Williams & Molina 11461* (F, GH).

10. Saurauia pringlei Rose, Contr. U. S. Nat. Herb. **7:** 52, 1903. (Type: *Pringle 4668*)

S. pringlei var. *micrantha* Busc., Malpighia **26:** 137, 1913. (Type: *Galeotti 3113*)
S. wildemanii Busc., loc. cit. 143. (Type: *Galeotti 3088*)
S. buscalioniana Blake, Contr. Gray Herb. **52:** 74, 1917. (Type: *Langlassé 1004*)

Shrubs and trees to 9 m; copiously to sparingly pubescent. *Leaf* blades narrowly elliptic to obovate, acute to acuminate, the base acute to obtuse, sometimes oblique, the margins serrate to serrulate, 9-26 cm long, 2-9 cm wide, chartaceous, the secondary veins 9-18 pairs, the tertiary veins elevated, more prominent than the lesser reticulation, abundantly setulose to sparingly tuberculate between the veins above, densely dendroid to sparingly stellate between the veins beneath, villous-barbate in the axils of the secondary veins beneath; petioles 1-3 cm long, 2-3 mm in diam. *Inflorescences* 10- to 37-flowered, 7-12 cm long, 3-7 cm wide, the primary peduncle 3-8 cm long, the bracts linear to triangular, 1-3 mm long. *Flowers* 11-14 mm broad, buds to 3-5 mm in diam, the pedicels 1-7 mm long at anthesis; sepals usually 5, 1-3 mm long, 1-3 mm wide, the inner 2 medially sparingly strigillose under more conspicuous stellate pubescence, laterally glabrous, ciliate, the imbricate sepal sparingly strigillose under more conspicuous stellate pubescence on the exterior half, glabrous, ciliate on the interior half, the outer 2 sparingly strigillose under more conspicuous stellate pubescence, all glabrous within; petals usually 5, white, usually obovate, 4-6 mm long, 2-4 mm wide, obtuse to incised at the apex; stamens 22-27, the anther 1.0-1.5 mm long, the filament 1.5-2.0 mm long; ovary 5-locular, globose, 5-sulcate, glabrous, the styles 5, obsolete to 1.5 mm long, the stigmas simple to subcapitate. *Fruit* not seen.

Barranca, by streamlet, sunny, wet canyon, western slopes; 1800-2800 m; flowering from March through July.

MEXICO: GUERRERO: Toro Muerto Mina, *Hinton 14212* (MICH, NY, US); Yesceros, Mina, *Hinton 14404* (MICH, NY, US); Omilteme, *Nelson 7051* (GH, US); second ridge W of Petlacala, *Mexia 9051* (F, GH, MO, NY, US). OAXACA: *Galeotti 3113* (BR), *s.n.* (F); *Liebmann 375B* (F); Juquila, *Galeotti 3088* (BR); Lactopa [Lacova?] *Liebmann 369* (F, US); Sierra de San Felipe, *Pringle 4668* (A, F, GH, NY, US); Mt Zempoaltepec, *Nelson 606* (US). WITHOUT PRECISE LOCALITY: Michoacan & Guerrero, *Langlassé 1004* (F, GH, US).

Galeotti used the number *3088* for two different collections, one from Juquila in Oaxaca and the other from Jalapa in Vera Cruz. Buscalioni based his *Saurauia wildemanii* on the former. He also annotated a specimen of this collection as *S. willdenowii*. Hooker based his *S. barbigera*, a synonym of *S. leucocarpa*, on the latter collection.

Blake differed with Buscalioni on his determination of *Langlassé 1004*. The plant is more robust, the leaves, flowers and trichomes somewhat larger than for the population as a whole; however, the collection falls within the geographical range of *S. pringlei* and except for larger dimensions agrees morphologically with the other collections.

11. SAURAUIA OREOPHILA Hemsl., Diag. Pl. Nov. 3, 1878. (Type: *Salvin s.n.*)

S. latipetala Hemsl., loc. cit. 4. (Type: *Ghiesbreght 646*)
S. pauciflora Rose, Contr. U.S. Nat. Herb. **8:** 52, 1903. (Type: *Nelson 3206*)
S. subalpina Donn. Sm., Bot. Gaz. **42:** 292, 1906. (Type: Donn. Sm. Pl. Guat. 2171)
S. oreophila f. *genuina* Busc., Malpighia **26:** 142, 1913, nom. nud.
S. oreophila f. *rubra* Busc., loc. cit., nom. subnud. (Type: *Salvin s.n.*)
S. pauciflora var. *ghiesbreghtii* Busc., loc. cit. 291, 1913. (ex char.; Type: *Ghiesbreght 606*, not seen)
S. parviflora var. *ghiesbreghtii* Busc., loc. cit. **27:** 302, 1916, nom. nud.

Shrubs and trees to 8 m; copiously to sparingly pubescent. *Leaf* blades narrowly elliptic to obovate, acuminate to acute, the base acute to obtuse, frequently oblique, the margins serrulate, 7-21 cm long, 2-6 cm wide, chartaceous, the secondary veins 9-23 pairs, the tertiary veins elevated, more prominent than the lesser reticulation, the epidermis frequently pustulate, abundantly to sparingly strigose to setulose between the veins above, abundantly stellate and minutely sericeous to nearly glabrous between the veins beneath, frequently villous-barbate in the axils of the secondary veins beneath; petioles 1-4 cm long, 1-2 mm in diam, terete to canaliculate above. *Inflorescences* 1- to 20-, rarely 30-flowered, 2-11 cm long, 1-5 cm wide, the primary peduncle 2-6 cm long, the bracts linear to triangular, 2-8 mm long, rarely foliaceous, 30 mm long. *Flowers* 15-22 mm broad, buds to 4-6 mm in diam, the pedicels to 4-17 mm long; densely to abundantly shaggy-hirtellous and stellate; sepals 5, rarely 6, 3-6 mm long, 2-6 mm wide, the inner 2 medially abundantly strigose or shaggy-strigillose and appressed-stellate, laterally glabrous, ciliate, the imbricate sepal abundantly strigose or shaggy-strigillose and appressed-stellate on the exterior half, glabrous, ciliate on the interior half, the outer 2 abundantly strigose or shaggy-strigillose and appressed-stellate, all glabrous within; petals 5, white, rarely pink, oblong to obovate, 7-9 mm long, 4-6 mm wide, obtuse to incised at the apex; stamens 21-24, the anther 2.0-2.5 mm long, the filament 2.0-2.5 mm long; ovary 5-locular, globose, 5-sulcate, glabrous, the styles 5, obsolete to 5 mm long, the stigmas simple to capitate. *Berries* 5-12 mm in diam, globose to ellipsoid, 5-sulcate, glabrous.

Cloud forest, wet forest, slopes, bushy hillside, bushy thicket; 2100-3300 m; flowering throughout the year.

Vernacular name: *Moco* (Guatemala—Standley)

Mexico: chiapas: *Ghiesbreght 646* (GH, MO, NY); nr San Cristóbal, *Nelson 3206* (GH, US).

Guatemala: chimaltenango: Chichavac, *Skutch 653* (A, F, US); "Santa Elena," *Skutch 153* (A, US); Las Calderas, *Standley 57805* (A, F). quiché: Nebaj, *Skutch 1741* (A, F, NY, US), *1745* (A, F); San Miguel Uspantán, *Heyde & Lux 2946* (GH, NY, US). sacatepéquez: V. Agua, *Smith 2171* (GH); San Rafael, *Smith 1326* (GH, NY, US); above Santa María de Jesús, *Standley 65057* (F), *65088* (F), *65279* (F). sololá: San Lucas, *Kellerman s.n.* (US); Inter Godinez et S. Lucas, *Bernoulli & Cario 3294* (K). without precise locality: V. Fuego, *Salvin s.n.* (K); San Martín, *Johnston 1306* (F).

12. Saurauia zahlbruckneri Busc., Malpighia **29:** 433, 1923. (Type: *Türckheim II1286*)

Shrubs and trees to 13 m; copiously to sparingly pubescent. *Leaf* blades narrowly elliptic to obovate, acuminate to acute, the base acute to obtuse, the margins minutely serrulate, 7-27 cm long, 2-11 cm wide, chartaceous to subcoriaceous, the secondary veins 10-23 pairs, the tertiary veins elevated, more prominent than the lesser reticulation, glabrous to abundantly sericeous between the veins above, glabrous or abundantly to sparingly hirsute between the veins beneath except the villous-barbate or cottony axils of the secondary veins; petioles 1-5 cm long, 1-3 mm in diam, flattened to canaliculate above. *Inflorescences* 10- to 50-flowered, 5-21 cm long, 2-10 cm wide, the primary peduncle 3-11 cm long, the bracts linear to triangu-

lar, 3-10 mm long. *Flowers* 12-19 mm broad, buds to 4-8 mm in diam, the pedicels to 3-10 mm long; sepals 5, 4-5 mm long, 4-5 mm wide, the inner 2 medially abundantly strigillose or hirsute-hirtellous and sometimes also filiform, laterally glabrous, ciliate, the imbricate sepal abundantly strigillose or hirsute-hirtellous and sometimes also filiform on the exterior half, glabrous, ciliate on the interior half, the outer 2 abundantly strigillose or hirsute-hirtellous and sometimes also filiform, all glabrous, rarely subapically pubescent within; petals 5, white, oblong, obovate or nearly circular, 5-10 mm long, 4-7 mm wide, obtuse to incised; stamens 30-35, the anther 2.0-2.5 mm long, the filament 2.5 mm long; ovary 5-locular, globose, 5-sulcate, glabrous, the styles 5, obsolete to 5 mm long, the stigmas simple to subcapitate. *Fruit* not seen.

Along road, barranca, wet thicket, forested slopes bordering streams, second growth, rich dense forest, wet forest, cloud forest, damp limestone thickets; 200-2500 m; flowering throughout the year.

MEXICO: CHIAPAS: Cerro del Boquerón, *Purpus 7014* (US); Mt Ovando, *Matuda 0441* (MICH, US); Mt Pasitar, *Matuda 1010* (A, MICH, MO); Siltepec, *Matuda 4089* (A, F, MICH, NY); Saxchanal, *Matuda 17809* (F).

GUATEMALA: ALTA VERAPAZ: Chamá to Cobán, *Johnson 565* (US); region of Chelac, NE of San Pedro, Carchá, *Standley 70394* (F); vic of Cobán, *Standley 89930* (F); Cobán, *Türckheim 2467* (US), *II1286* (F, GH, NY, US); nr Cobán, *Standley 71596* (F); Saquijá, 43 km NE of Cobán, *Standley 70145* (F); nr Senahú, *Cook & Doyle 37* (US); ca 8 km below Tactic, *Standley 90544* (F). HUEHUETENANGO: betw Ixcán & Finca San Rafael, *Steyermark 49421* (A, F); vic of Nucapoxlac, *Steyermark 48953* (F).

The Mexican collections, with petioles, peduncles and leaves generally more pubescent, differ markedly from the Guatemalan. The cottony border of the midrib of mature leaves, so conspicuous in Guatemalan specimens, is lacking in the Mexican; however, in the latter, the axils of the secondary veins on the underside of the leaves are villous-barbate. Although there is a tendency to shed the juvenile foliar pubescence in the latter, the tendency is less pronounced than in the Guatemalan plants. The deep wine-red color of the petioles, peduncles and major veins of dried specimens is a helpful characteristic for purposes of identification.

13. SAURAUIA ASPERA Turcz., Bull. Soc. Nat. Moscou **31:** Partie 1: 242, 1858, (Type: *Galeotti* 7325)

S. aspera f. *delessertiana* Busc., Malpighia **27:** 303, 1916. (Type: *Galeotti* 7325)
S. englesingii Standl., Field Mus. Publ. Bot. **4:** 233, 1929. (Type: *Englesing 281*)
S. perseifolia Standl. & Steyerm., loc. cit. **23:** 216, 1947. (Type: *Steyermark 41784*)

Trees to 15 m; copiously pubescent with trichomes usually shorter than 2 mm. *Leaf* blades obovate to elliptic, acute to acuminate, the base obtuse, frequently oblique, the margins setaceo-serrulate, 9-34 cm long, 4-14 cm wide, chartaceous, the secondary veins 19-25 pairs, the tertiary veins elevated, more prominent than the lesser reticulation, abundantly setulose, strigillose, hirsute or hirtellous between the veins above, abundantly hirsute to hirtellous between the veins beneath, villous-barbate in the axils of the secondary veins beneath; petioles 1-3 cm long, 1-4 mm in diam, terete to somewhat canaliculate above. *Inflorescences* 35- to 100-flowered, 6-24 cm long, 6-11 cm wide, the primary peduncle 1-14 cm long, the bracts linear

to triangular, 1-5 mm long. *Flowers* 11-14 mm broad, buds to 3-5 mm in diam, the pedicels 1-10 mm long; sepals 5, 3-5 mm long, 3-4 mm wide, the inner 2 medially densely shaggy-strigillose or hirtellous mixed with smaller trichomes, laterally appressed-pubescent, submarginally glabrous, ciliate, the imbricate sepal densely shaggy-strigillose or hirtellous mixed with smaller trichomes on the exterior half, appressed-pubescent, submarginally glabrous, ciliate on the interior half, the outer 2 densely shaggy-strigillose or hirtellous mixed with smaller trichomes, all glabrous within except the subapically pubescent outer and imbricate sepals; petals 5, white to pink, oblong to obovate, 5-7 mm long, 3-5 mm wide, obtuse to incised at the apex; stamens 33-41, the anther 2.0-2.5 mm long, the filament 2.0-3.0 mm long; ovary 5-locular, globose, 5-sulcate, glabrous, the styles 5, obsolete to 3 mm, the stigmas simple to subcapitate. *Berries* 6-8 mm in diam, globose, 5-sulcate, glabrous.

Dense forest, along river, wet thicket and bushland; 20-2000 m; flowering from December to August.

MEXICO: CHIAPAS: Escuintla, *Matuda 16809* (F, NY); Mt Ovando, *Matuda 0642* (A, F, MICH, MO, NY). OAXACA: *Galeotti 7235* (US). VERA CRUZ: Minatitlan, *Andrieux 199* (K).
GUATEMALA: IZABAL: Cerro San Gil, along Río Tameja, *Steyermark 41784* (F, US). WITHOUT PRECISE LOCALITY: in Finca Santa Inés, *Record & Kuylen* G79 (GH, US).
HONDURAS: ATLÁNTIDA: vic of La Ceiba, *Yuncker et al. 8689* (F, GH, MO, NY, US); nr Tela, *Standley 53521* (A, F, US). WITHOUT PRECISE LOCALITY: *Bangham 322* (A, F); mts back of Puerto Sierra, *Wilson 171* (NY, US); San Pedro Sula, *Salvoza 831* (A).
NICARAGUA: WITHOUT PRECISE LOCALITY: Braggman's Bluff, *Englesing 281* (A, F, GH, NY); 200 mi up Wanks River, *Schramm s.n.* (F).

In spite of its broad distribution, *S. aspera* is rather poorly represented in herbaria. It is distinguished from *S. scabrida,* which it resembles, by a lack of stellate pubescence on the lower surface of its leaves which are villous-barbate in the axils of the secondary veins beneath.

The Mociño, Sessé & Moldonado collection, *4802,* a photo of which I have seen, is also representative of this population.

The Gray Herbarium card index lists *S. parviflora* var. *ghiesbrechti* f. *delessertiana* Busc. (Malpighia **27:** 303, 1916). This is an incorrect notation of *S. aspera* f. *delessertiana* Busc. (loc. cit.).

14. SAURAUIA SELERORUM Busc., Malpighia **26:** 100, 1913. (Type: *Seler 2819*)

Shrubs and trees to 13 m; copiously pubescent with trichomes frequently longer than 2 mm, but never paleaceous. *Leaf* blades narrowly to broadly elliptic to obovate, rarely broadly subobtrullate, acute to acuminate, rarely obtuse, the base acute to obtuse, sometimes oblique, the margins setaceo-serrulate, 12-48 cm long, 4-18 cm wide, chartaceous to subcoriaceous, the secondary veins 15-30 pairs, the tertiary veins elevated, more prominent than the lesser reticulation, the pubescence densely to abundantly setose-setulose between the veins above, densely to abundantly loriform, hirsute or hirtellous and sometimes also stellate between the veins beneath; petioles 1-9 cm long, 2-5 mm in diam, flattened to canaliculate above. *Inflorescences* 30- to 175-flowered, 6-35 cm long, 2-11 cm wide, the primary peduncle 3-23 cm long, the bracts linear to triangular, 2-10 mm long, rarely foliaceous,

to 25 mm long. *Flowers* 14-22 mm broad, buds to 4-7 mm in diam, the pedicels 2-25 mm long; sepals 5, sometimes 6, 3-5 mm long, 3-5 mm wide, the inner 2 medially densely to abundantly hirsute to hirtellous and sometimes also stellate, laterally glabrous, ciliate, the imbricate sepal densely to abundantly hirsute to hirtellous and sometimes also stellate on the exterior half, glabrous, ciliate, on the interior half, densely to abundantly hirsute to hirtellous and sometimes also stellate, all glabrous within; petals 5, sometimes 6, white to pinkish, 7-10 mm long, 4-8 mm wide, obtuse to incised at the apex; stamens 23-35, the anther 2.0-2.5 mm long, the filament 2.0-2.5 mm long; ovary 5- sometimes 4-locular, globose, 4- to 5-sulcate, glabrous, the styles 4-5, obsolete to ca 4 mm long, the stigmas simple to capitate. *Berries* 7-10 mm in diam, globose, 4- to 5-sulcate, glabrous.

Densely mixed forest on white sand slopes, densely wooded damp barranca, wet slopes of forested ravine along stream, moist oak-forest, cutover land, cloud forest, upper rocky slopes, near waterfall, deep woods; 600-4038 m; flowering throughout the year.

Vernacular names: *Moco, Moquillo* (Guatemala—Standley); *Zapote de Montaña* (El Salvador—Carlson); *Mocoso* (Honduras—Standley), *Pacón* (Honduras—Edwards).

MEXICO: CHIAPAS: Cerro del Boquerón, *Purpus 7013* (A, F, GH, MO, NY, US); Los Lagos, 34 mi SE of Comitán, *Carlson 2299* (F); Motozintla, *Matuda 15515* (F); Mt Pasitar, *Matuda 1003* (A, F, MICH, MO), *1694* (A, F, K, NY, MICH, MO); Mt Tacaná, *Matuda 2301* (A, F, MICH, NY), *2947* (F, MICH).

GUATEMALA: CHIMALTENANGO: Chichavac, *Skutch 405* (A, F, US), *410* (A, F, US). CHIQUIMULA: nr Amatillo, *Steyermark 30532* (F). GUATEMALA: Finca La Aurora, *Aguilar 484* (F). HUEHUETENANGO: San Juan Ixcoy, *Steyermark 50014* (F); San Martín, *Seler & Seler 2819* (GH, US). JUTIAPA: V. Suchitán, NW of Asunción Mita, *Steyermark 31911* (F). QUEZALTENANGO: V. Zunil, at & above Aguas Amargas, *Standley 65358* (A, F); above Mujuliá, betw San Martín Chile Verde & Colomba, *Standley 85542* (F); region of Las Nubes, *Standley 83602* (F); El Pocito, S of San Martín Chile Verde, on road to Colomba, *Standley 84897* (F); W slope of V. Zunil, *Standley 67375* (F); V. Zunil, *Steyermark 34780* (F). SAN MARCOS: San Marcos, *Standley 66197* (F); above San Rafael Pié de la Cuesta, *Standley 68645* (F); betw Sibinal & Canjula, V. Tacaná, *Steyermark 36037* (F, NY). SUCHITEPÉQUEZ: Santa Clara, *Steyermark 46657* (F, NY). ZACAPA: vic of Finca Alejandria, Sierra de las Minas, *Steyermark 29881* (F); Río Lima, Sierra de las Minas, *Steyermark 30036* (F); Sierra de las Minas, along Río Repollal, *Steyermark 42548* (F).

EL SALVADOR: SANTA ANA: nr Metapan, *Carlson 755* (F); Montecristo, *Allen & Severen 7120* (F).

HONDURAS: INTIBUCÁ: vic of La Esperanza & Intibucá, *Standley 25225* (F). MORAZAN: Las Flores, *Standley 13246* (F); Mt San Juancito, *Glassman 1987* (F, NY); above San Juancito, *Hawkes et al. 2046* (F); SW of San Juancito, *Williams & Molina 12799* (F); Mt Uyuca, *Allen 4009* (MO); *Glassman 2035* (F, NY); *Pfeifer 1419* (MO), *1452* (MO); *Standley & Williams 672* (F); *Valerio 738* (F); *Williams & Molina 10276* (A, F, MO); *Carlson 2467* (F). STA. BARBARA: upper rocky slopes & summit of Cerro de Sta. Barbara, *Allen et al. 6076* (F, US). TEGUCIGALPA: Rosario, *Edwards 52* (A).

Saurauia scabrida, sympatric with *S. selerorum* throughout the range of the latter, has long been identified with it under the name *S. villosa*. Standley & Steyermark (1949) were correct in treating the two populations as distinct. For the former, they used the name *S. villosa;* they called the latter *S. subalpina*, an obscure synonym of *S. oreophila*, which had not been used since its publication.

Over most of its range, *S. selerorum* is distinguished from *S. scabrida* by longer

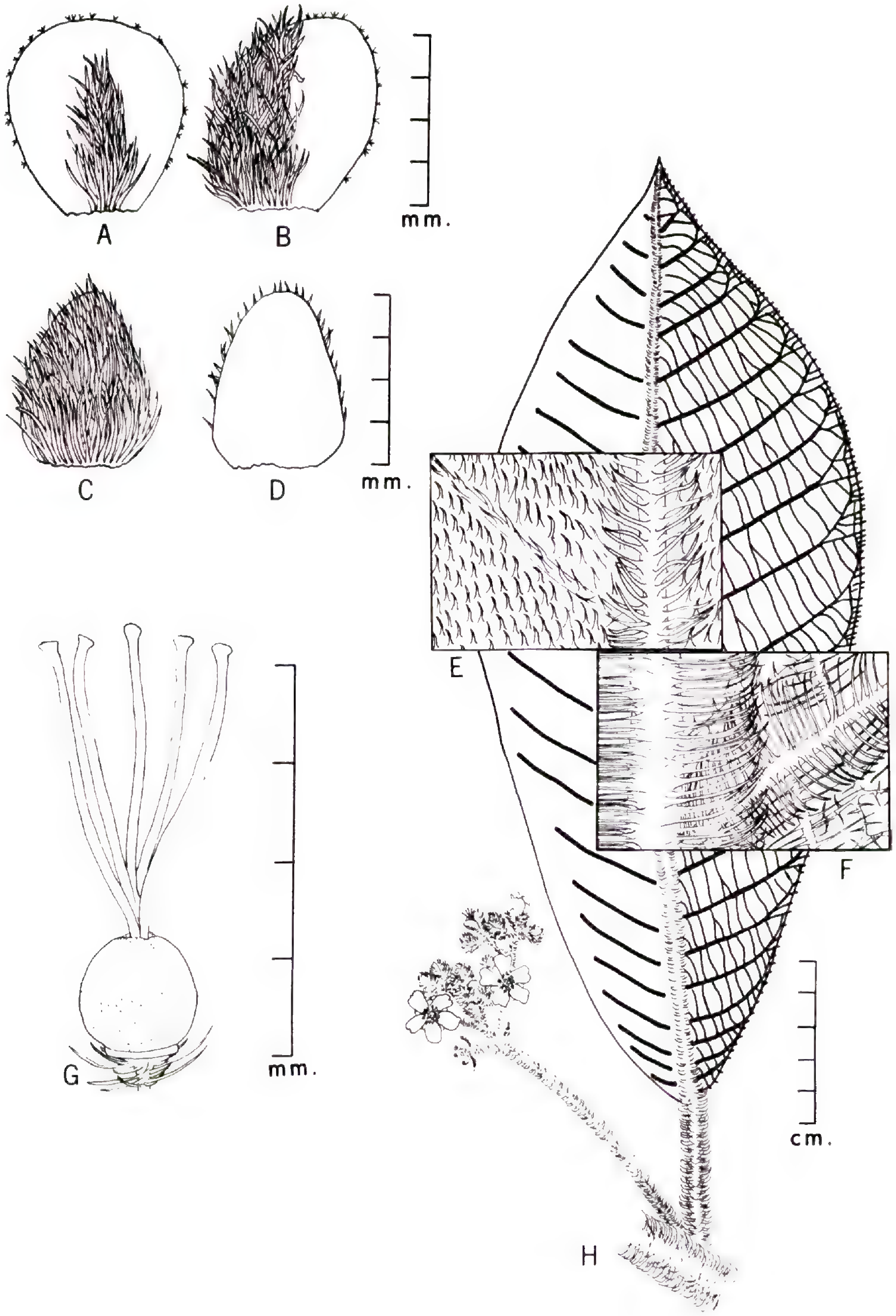


Fig. 4. *S. selerorum.* A. Inner sepal, outer surface; B. Imbricate sepal, outer surface; C. Outer sepal, outer surface; D. Outer sepal, inner surface; E. Upper leaf surface; F. Lower leaf surface; G. Ovary; H. Leaf and inflorescence.

multicellular unbranched hairs and a lack of stellate pubescence on the lower leaf surface. In Mexico and western Guatemala, however, the leaves may be quite stellate beneath and the sepals, which are not usually pubescent within, are sometimes submarginally pubescent.

15. SAURAUIA CONZATTII Busc., Malpighia **25:** 403, 1913. (Type: *Conzatti & Cancino 2433*)

S. matudai Lundell, Contr. Univ. Mich. Herb. **7:** 27, 1942. (Type: *Matuda 4339*)
S. cuchumatanensis Standl. & Steyerm., Field Mus. Publ. Bot. **23:** 215, 1947. (Type: *Steyermark 49810*)

Shrubs and trees to 7 m; copiously pubescent, sometimes paleaceous. *Leaf* blades elliptic to obovate, acuminate, the base acute to obtuse, sometimes oblique, the margins serrulate to setaceo-serrulate, 11-27 cm long, 5-10 cm wide, membranaceous to subcoriaceous, the secondary veins 11-24 pairs, the tertiary veins elevated, more prominent than the lesser reticulation, abundantly hirsute to sericeous or glabrescent between the veins above, abundantly hirsute to sericeous or glabrous between the veins beneath, not barbate in the axils of the secondary veins beneath; petioles 1-4 cm long, 1-3 mm in diam, flattened to canaliculate above. *Inflorescences* 6- to 67-flowered, 7-21 cm long, 2-11 cm wide, the primary peduncle 5-13 cm long, the bracts linear, 2-17 mm long. *Flowers* 15-25 mm broad, buds to 5-7 mm in diam, the pedicels 5-13 mm long; sepals 5, 3-5 mm long, 2-5 mm wide, the inner 2 medially abundantly hirsute, laterally glabrous, ciliate, the imbricate sepal abundantly hirsute on the exterior half, glabrous, ciliate on the interior half, the outer 2 abundantly hirsute, all glabrous within; petals 5, white, oblong to obovate, 6-9 mm long, 3-7 mm wide, obtuse to incised at the apex; stamens 13-29, the anther 1.5-2.5 cm long, the filament 2.0-2.5 cm long; ovary 5-, rarely 4-locular, globose, 5-, rarely 4-sulcate, glabrous, the styles 5, rarely 4, obsolete to 3 mm long, the stigmas simple to capitate. *Berries* 6 mm in diam, globose, 5- rarely 4-sulcate, glabrous.

Advanced forest, dark rain forest, limestone area; 1500-3000 m; flowering in January and June to August.

Vernacular names: *Ma-gwa-ni, Mameyito* (Oaxaca—Schultes).

MEXICO: CHIAPAS: Letrero, nr Siltepec, *Matuda 4339* (A, MO, NY); Laguna Ocotal Grande, 45 km E of Ocosingo, *Dressler 1464* (GH, NY, US). OAXACA: Cuyamecalco, Cuicatlán, *Conzatti 2337* (F), *Conzatti & Cancino 2433* (US); betw San Pedro Yolox & Tepetotutla, *Schultes 695* (GH, US); Zantla, *Conzatti & Gonzales 773* (GH). WITHOUT PRECISE LOCALITY: *Liebmann 364* (F); Totulipa, *Liebmann 366* (F).

GUATEMALA: ALTA VERAPAZ: Chicoyou, Cobán, *Hatch & Wilson 229* (F). HUEHUETENANGO: Cerro Huitz, betw Mimanhuitz & Yulhuitz, Sierra de los Cuchumatanes, *Steyermark 48560* (F, GH); Cruz de Limon, betw San Mateo Ixtatan & Nuca, *Steyermark 49810* (F), *49865* (A, F, NY).

Some plants of *S. conzattii* bear the most robust of all the trichomes found on specimens of North American species of *Saurauia.* Although they are frequently shed on the upper leaf surface, the paleaceous or hirsute trichomes remain conspicuous on the petioles, peduncles and young branch tips. *Steyermark 49865* differs from the other collections in having smaller leaves and flowers, as well as scattered-hirtellous sepals.

16. Saurauia pedunculata Hook., Ic. Pl. **4:** *t. 341-342,* 1841. (ex icon.)

S. pedunculata f. *veranii* Busc., Malpighia **28:** 236, 1917. (Type: *Pringle 8105*)
S. pedunculata var. *leucocarpa* Busc., loc. cit. 237. (ex char.; Type: *Satorius 5409,* not seen)
S. pedunculata var. *leucocarpa* f. *veranii* Busc., loc. cit. 315, 1918. (Type: *Bourgeau 2060*)

Trees to 6 m, sparingly pubescent. *Leaf* blades elliptic to obovate, acute to acuminate, the base acute to obtuse, the margins serrulate, 10-24 cm long, 3-11 cm wide, chartaceous, the secondary veins 17-22 pairs, the tertiary veins elevated, more prominent than the lesser reticulation, scattered-strigillose between the veins above, glabrous between the veins beneath, villous-barbate in the axils of the secondary veins; petioles 1-5 cm long, 1-3 mm in diam, flattened to canaliculate above. *Inflorescences* 18- to 78-flowered, 10-24 cm long, 3-9 cm wide, the primary peduncle 6-12 cm long, the bracts foliaceous or linear to triangular, 1-25 mm long. *Flowers* 12-15 mm broad, buds to 4-7 mm in diam, the pedicels to 3-11 mm long; sepals 5, 4-5 mm long, 3-5 mm wide, the inner 2 medially densely hoary-pubescent with minute branched trichomes, sub-marginally glabrous, ciliate, the imbricate sepal densely hoary-pubescent with minute branched trichomes on the exterior half, submarginally glabrous, ciliate, the imbricate sepal densely hoary-pubescent with minute branched trichomes on the exterior half, submarginally glabrous, ciliate on the interior half, the outer 2 densely hoary-pubescent with minute branched trichomes, all glabrous within except the subapically pubescent outer and imbricate sepals; petals 5, white, oblong to obovate, 7-8 mm long, 4-6 mm wide, obtuse to incised at the apex; stamens 28-42, the anther 2.0-2.5 mm long, the filament 2.0-3.0 mm long; ovary 5-locular, globose, 5-sulcate, glabrous, the styles 5, obsolete to 4 mm long, the stigmas simple to capitate. *Berries* 8 mm in diam, globose, glabrous.

Along streams, moist rocky localities, rocky banks, forest; 900-1500 m; flowering throughout the year.

Mexico: oaxaca: *Ghiesbreght 75* (F). vera cruz: Acultzinco, *Matuda 1150* (A, F, MICH, MO, NY); Valle de Cordova, *Bourgeau s.n.* (F), *2060* (P), *2241* (GH); Jalapa, *MacDaniels 938* (F); Mt Mecaltepec nr Jalapa, *Pringle 7749* (GH); nr Jalapa, *Pringle 8105* (A, F, GH, MO, NY, US), *Schiede & Deppe s.n.* (HAL), *327* (HAL, NY), *456* (HAL), *Smith 1546* (F), *Rose & Hough 4279* (NY, US); Mirador, *Liebmann 365* (F), *375A* (F); Orizaba, *Botteri 110* (GH), *248* (A, F, GH, US), *Bourgeau 3221* (NY, US), *Mohr & Botteri s.n.* (US), *s.n.* (US), *Müller s.n.* (NY), *979* (NY); Zacualpan, *Purpus s.n.* (A), *287* (A), *2225* (F, GH, MO, NY, US), *10829* (US), *14156* (A), *16692* (US).

17. Saurauia serrata DC., Mém. Soc. Phys. Genève **1:** 420, 1822. (ex icon.)

Leucothea serrata Moc. & Sessé ex DC., loc. cit., nom. nud.
Davya serrata Moc. & Sessé ex DC., Prodr. **1:** 526, 1824, nom. nud.
Coriaria cuneifolia Sessé & Moc., Pl. Nov. Hisp. 173, 1890. (ex char.)
Saurauia reticulata Rose, Contr. U. S. Nat. Herb. **8:** 52, 1903. (Type: *Pringle 7862*)
S. pedunculata Hook. var. *fluviatilis* Busc., Malpighia **25:** 12, 1912, nom. subnud. (Type: *Pringle 10122*)
S. pedunculata var. *reticulata* Busc., loc. cit., nom. subnud. (Type: *Pringle 7862*)
S. pedunculata var. *strigillosa* Busc., loc. cit., nom. subnud. (Type: *Langlassé 702*)
S. pseudopringlei Busc. var. *fluviatilis* Busc., loc. cit. **28:** 380, 1919 (Type: *Pringle 10122*)
S. fluviatilis Rose ex Busc., loc. cit. (Type: *Pringle 10122*)
S. pseudopedunculata Busc., loc. cit. 398, (Type: *Langlassé 702*)

Trees to 15 m; usually sparingly pubescent. *Leaf* blades narrowly elliptic to obovate, acute to acuminate, the base acute to obtuse, the margins serrulate, 10-30 cm long, 4-12 cm wide, chartaceous, the secondary veins 14-26 pairs, the tertiary veins elevated, more prominent than the lesser reticulation, scattered-strigillose, rarely abundantly minutely sericeous between the veins above, scattered to sparingly minutely sericeous between the veins beneath, frequently villous-barbate in the in the axils of the veins beneath; petioles 1-4 cm long, 1-3 mm in diam., flattened to canaliculate above. *Inflorescences* 12- to 56-flowered, 6-20 cm long, 2-12 cm wide, the primary peduncle 2-10 cm long, the bracts linear to triangular, 1-10 mm long, rarely foliaceous, to 35 mm long. *Flowers* 13-24 mm broad, buds to 4-7 mm in diam, the pedicels to 3-15 mm long, rarely longer; sepals 5, 3-5 mm long, 3-5 mm wide, the inner 2 medially abundantly to sparingly shaggy-strigillose, rarely densely hirsute or sericeous, laterally glabrous, margins ciliate, the imbricate sepal abundantly to sparingly shaggy-strigillose, rarely densely hirsute or sericeous on the exterior half, glabrous, ciliate on the interior half, the outer 2 abundantly to sparingly shaggy-strigillose and stellate, rarely densely hirsute or sericeous, all glabrous, rarely subapically pubescent within; petals 5, white, rarely pinkish, oblong to obovate, 7-9 mm long, 3-5 mm wide, rarely larger, obtuse to incised at the apex; stamens 16-33, the anther 2.0-3.0 mm long, the filament 2.0-3.5 mm long; ovary 5-locular, globose, 5-sulcate, glabrous, the styles 5, obsolete to 5 mm long, the stigmas simple to capitate. *Berries* to 8-12 mm in diam, globose, 5-sulcate, glabrous.

In the water, barrancas, by streams, oak-forest, pine-forest, podocarp-forest, hills; 400-2500 m; flowering throughout the year.

Vernacular names: *Mameyito* (Oaxaca--Reko); *Níspero* (Guerrero—Hinton).

MEXICO: GUERRERO: Galeana, *Hinton 10812* (F, GH, MO, NY, US), *14737* (GH, NY, US); Mina, *Hinton 10700* (GH), *10748* (F, GH, MO, NY, US), *14958* (GH, NY, US); Vallecitos, *Hinton 11342* (NY, US). JALISCO: SW of Talpa de Allende, *McVaugh 14402* (MICH, MO); 11-12 mi S of Talpa de Allende, *McVaugh 21413* (MICH, MO); below pass to Talpa de Allende, *McVaugh 20316* (MICH, MO); betw Tecalitlán & San Isidro nr a lumber rd, *McVaugh 15018* (MICH, MO). MICHOACÁN: Coahuayana, *Hinton 16257* (MICH, NY, US); Mt La Cruz, *Storm 1939* (US); Uruápan, *Pringle 10122* (F, GH, MICH, MO, NY, US). MORELOS: nr Cuernavaca, *Pringle 7862* (GH, US). NAYARIT: ca 10 rd mi E of Jalcocotán, *McVaugh 12097* (MICH, MO); 9.5 mi W of Tepic, *McVaugh 18972* (MICH, MO); hills back of Jalisco, *Ferris 5974* (A, F, NY, US). OAXACA: vic of Cafetal Condordia, *Morton & Makrinius 2415* (US); *Morton 2460* (US); Cafetal Concordia, *Reko 3707* (US); Juquila, *Conzatti 4530* (US); Pochutla, *Reko 6318* (F); Finca La Soledad, *Carlson 2712* (F). SINALOA: Tres Hermanos, *Dehesa 1544* (US). TEMASCALTEPEC: Nanchititla, *Hinton 3597* (A, NY), *5322* (F, US), *7358* (GH, NY, US). WITHOUT PRECISE LOCALITY: Sierra Madre, Michoacán & Guerrero, *Langlassé 702* (F, GH, K, US).

Throughout its broad range, *S. serrata* is influenced by neighboring or sympatric populations. In the north, it resembles *S. pedunculata;* in the middle of its range, *S. pringlei;* in the south, *S. aspera.* Thus, its leaves, which are usually nearly as glabrous as those of *S. pedunculata* above, may become abundantly sericeous. In addition, the multicellular unbranched hairs of the sepals vary considerably in both size and density.

18. Saurauia angustifolia Turcz., Bull. Soc. Nat. Moscou **31,** Partie 1: 242, 1858. (Type: *Jürgensen 898*)

S. anisopoda Turcz., loc. cit. (Type: *Galeotti 4198*)
S. leucocarpa Schlecht. var. *stenophylla* Busc., Malpighia **29:** 104, 1921. (Type: *Seler 3103*)
S. leucocarpa var. *stenophylla* f. *veranii* Busc., loc. cit. 107. (Type: *Seler 3103*)
S. leucocarpa var. *anisopoda* Busc., loc. cit. (Type: *Galeotti 4198*)
S. leucocarpa var. *angustifolia* Busc., loc. cit. 112. (Type: *Jürgensen 898*)

Shrubs and trees to 10 m; sparingly pubescent. *Leaf* blades narrowly elliptic to obovate, acuminate to acute, the base acute to obtuse, the margins serrulate, 9-17 cm long, 3-6 cm wide, chartaceous, the secondary veins 11-23 pairs, the tertiary veins elevated, more prominent than the lesser reticulation, scattered-strigillose to nearly glabrous between the veins above, scattered-strigillose between the veins beneath, not barbate in the axils of the secondary veins beneath; petioles 1-3 cm long, 1-2 mm in diam. *Inflorescences* 4- to 20-flowered, 4-10 cm long, 2-6 cm wide, the primary peduncle 2-5 cm long, the bracts linear to linear-triangular, 2-10 mm long. *Flowers* 14-17 mm broad, buds to 4-5 mm in diam, the pedicels 3-13 mm long; sepals 5, 3-5 mm long, 2-5 mm wide, the inner 2 medially abundantly to sparingly strigillose, laterally glabrous, ciliate, the imbricate sepal abundantly to sparingly strigillose, rarely glabrous on the exterior half, glabrous, ciliate on the interior half, the outer 2 abundantly to sparingly strigillose, rarely glabrous, all glabrous, rarely subapically pubescent within; petals 5, white, oblong to obovate, 6-7 mm long, 3-6 mm wide, obtuse to incised at the apex; stamens 17-19, the anther 1.5-2.5 mm long, the filament 1.5-2.5 mm long; ovary 5-locular, globose, 5-sulcate, glabrous, the styles 5, 3-5 mm long, the stigmas capitate. *Berries* 8-15 mm in diam, globose, 5-sulcate, glabrous.

Advanced forest, slopes, forested slopes, pine-covered canyon, pine-oak area, cloud forest; 1300-2400 m; flowering throughout the year.

Mexico: chiapas: Siltepec, *Matuda 4073* (A, MICH, NY). oaxaca: Sierra de San Pedro Nolasco, Talea de Castro [District of Villa Alta] *Jürgensen 898* (K). without precise locality: *Galeotti 4198* (F, US).

Guatemala: alta verapaz: nr San José, SE of Tactic, *Standley 69628* (F); Tactic, *Türckheim II700*, Donn. Sm. Pl. Guat. 8380 (F, GH, NY, US), *II723*, Donn. Sm. Pl. Guat. 8395 (GH, US). chimaltenango: Actenango, *Standley 61794* (A, F); above Las Calderas, *Standley 60077* (A, F). el progreso: betw Calera & middle slopes of quebradas of V. Siglo, *Steyermark 43000* (F). huehuetenango: Cerro Huitz, betw Mimanhuitz & Yulhuitz, *Steyermark 48661* (F); San Martín, *Seler & Seler 3103* (GH, US). jalapa: Aguacate, *Williams 13187* (F, GH); V. Jumay, *Steyermark 32324* (F). quezaltenango: V. Santa María, *Steyermark 34015* (F). zacapa: nr Finca Alejandria, Sierra de las Minas, *Steyermark 29806* (F), *30035* (F).

Saurauia angustifolia is distinguished from *S. oreophila* by the complete lack of stellate hairs on the undersurface of the leaves, even in the young stages.

Series IV

Laevigatae Busc., Malpighia **25:** 224, 1912, emend.

Barbigerae Busc., loc. cit. 223, pro parte.

a. Perianth usually 5-merous, broader than 12 mm (except the smaller, 3- to 5-carpellate *S. leucocarpa*).
  b. Leaves not barbate in the axils of the secondary veins beneath, the epidermis glabrous to scattered-pubescent above and beneath; sepals densely heterotrichous without, obscuring the margins, Panama .... 19. *S. seibertii*

bb. Leaves conspicuously villous-barbate in the axils of the secondary veins beneath; sepals glabrous or homotrichous.
c. Foliar veins scattered-strigose, the epidermis glabrous, pustulate, sepals glabrous; flower diam 7-12 mm, bud diam 2-4 mm. Mexico: Vera Cruz, Hidalgo, Puebla, Oaxaca, Chiapas; Honduras .... 20. *S. leucocarpa*
cc. Foliar veins scattered-tufted, the epidermis glabrous, epustulate; sepals glabrous to densely stellate; flower diam 15-25 mm, bud diam ca 5 mm. Mexico: Chiapas; Guatemala; El Salvador .... 21. *S. kegeliana*

aa. Perianth 4-merous (rarely 3- to 5-merous), 7-10 mm broad; leaves glabrous in the axils of the secondary veins beneath, the foliar veins scattered-tufted, the epidermis glabrous, pustulate; sepals densely stellate, becoming scattered-stellate to glabrous medially. Mexico: Oaxaca, Tabasco and Chiapas to South America .... 22. *S. laevigata*

19. Saurauia seibertii Standl., Ann. Missouri Bot. Gard. **26:** 290, 1939. (Type: *Woodson, Allen & Seibert 1020*)

Trees to 25 m; sparingly pubescent. *Leaf* blades elliptic to obovate, acute to acuminate, the base obtuse, the margins serrulate, 9-21 cm long, 3-8 cm wide, chartaceous, the secondary veins 10-18 pairs, the tertiary veins immersed, scarcely more prominent than the lesser reticulation, the veins sparingly tufted to glabrous above, abundantly to scattered-heterotrichous beneath, the epidermis scattered-tufted to glabrous above, scattered-clustered, glabrous in the axils of the secondary veins beneath; petioles 2-4 cm long, 1-2 mm in diam, flattened to canaliculate above. *Inflorescences* 26- to 52-flowered, rarely fewer, 13-28 cm long, 6-9 cm wide, the primary peduncle 6-15 cm long, the bracts linear to triangular, 2-8 mm long, sometimes foliaceous, to 50 mm long. *Flowers* 15-22 mm broad, buds to 6-7 mm in diam, the pedicels 5-20 mm long; sepals 5, 4-6 mm long, 3-6 mm wide, the inner 2 medially densely heterotrichous, laterally densely appressed-pubescent, the imbricate sepal densely heterotrichous on the exterior half, densely appressed-pubescent on the interior half, the outer 2 densely heterotrichous, all densely appressed-pubescent within; petals 5, white, oblong to obovate, 6-9 mm long, 3-8 mm, obtuse to incised at the apex; stamens 39, rarely ca 25, the anther 2.0-2.5 mm long, the filament 2.0-2.5 mm long; ovary 5-locular, globose, 5-sulcate, glabrous, the styles 5, obsolete to 4 mm long, the stigmas simple to capitate. *Berries* to 8 mm in diam, globose, 5-sulcate, glabrous.

Open sunlight, damp habitat, common along river, disturbed cloud forest; 1500-2300 m; flowering from May to August.

Vernacular name: *Avosatia* (Panama—G. White)

Panama: bocas del toro: Robalo trail, *Allen 4968* (MO). chiriquí: along Río Caldera, *Woodson et al. 1020* (A, F, K, MO, NY, US); Río Chiriquí Viejo valley, *White 151* (MO), *White 110* (MO); Boquete, Palo Alto, *Stern et al. 1075* (MO, US).

The specimen collected by Allen in Bocas del Toro is aberrant. It lacks the many-flowered lax inflorescence so characteristic of the other specimens, but agrees with them in the foliar clustered and tufted trichomes, the smooth leaves which are nearly glabrous above and the reticulating tertiary veins.

20. Saurauia leucocarpa Schlecht., Linnaea **10:** 249, 1836. (Type: *Schiede 330*)

S. barbigera Hook., Ic. Pl. **4:** *t. 331*, 1841. (Type: *Galeotti 3088*)
S. pedunculata Hook. var. *pringleana* Busc., Malpighia **25:** 12, 1912, nom. subnud. (Type: *H. & C. Conzatti & Cancino 2467*)
S. pseudopringlei Busc., loc. cit. **28:** 378, 1919. (Type: *H. & C. Conzatti & Cancino 2467*)
S. barbigera f. *veranii* Busc., loc. cit. 481, 1920. (Type: *Galeotti 3088*)
S. leucocarpa f. *veranii* Busc., loc. cit. **29:** 104, 1921. (Type: *Schiede 330*)
S. leucocarpa var. *wildemanii* Busc., loc. cit. 111. (Type: *Galeotti 3088*)

Shrubs and trees to 10 m; sparingly pubescent. *Leaf* blades obovate, acuminate, the base acute, often slightly oblique, the margins serrulate, 3-15 cm long, 2-5 cm wide, chartaceous, the secondary veins 6-12 pairs, the tertiary veins immersed, scarcely more prominent than the lesser reticulation, the veins sparingly to scattered-strigose, the epidermis pustulate, scattered-strigillose between the veins above, scattered minutely sericeous between the veins beneath, villous-barbate in the axils of the secondary veins beneath; petioles 0.5-2.0 cm long, 0.5-1.5 mm in diam. *Inflorescences* 7- to 65-flowered, 3-14 cm long, 1-5 cm wide, the primary peduncle 2-10 cm long, the bracts linear to triangular, 1-4 mm long. *Flowers* 7-12 mm broad, buds 2-4 mm in diam, the pedicels to ca 5 mm long, the sepals 5, sometimes 4 or 6, 2-3 mm long, 2-3 mm wide, glabrous, ciliate; petals 5, sometimes 4 or 6, white, obovate, 4-7 mm long, 3-4 mm wide, obtuse to incised at the apex; stamens 22-28, the anther ca 1 mm long, the filament ca 1.5 mm long; ovary 3- to 5-locular, globose, 3- to 5-sulcate, glabrous, the styles 3-5, 1-2 mm long, the stigmas simple to subcapitate. *Berries* globose, 3- to 5-sulcate, glabrous, to ca 15 mm in diam.

Moist mountain slopes, wooded ravines, wooded slopes, cloud zone, rain forest, canyon; 1300-2500 m; flowering throughout the year.

Vernacular names: *Cerbatana* (Honduras—Hagen), *Chaco* (Honduras—Molina).

Mexico: chiapas: Fenia, *Purpus 10025* (US), *10087* (US). hidalgo: betw Molango & Calnali, *Moore 3002* (GH); Chiconquiaco, *Schiede 330* (HAL, MO, NY). oaxaca: Coyula de Cuyamecalco Distrito de Cuicatlán, *Conzatti et al. 2467* (F, NY). puebla: ca 8 mi N of Teziutlán, *Manning & Manning 53914* (GH). vera cruz: Jalapa, *Galeotti 3088* (BR, K), *Hahn s.n.* (K), *Pringle 8201* (A, F, GH, MO, US), *9201* (GH, US); Maltrata, *Matuda 1198* (A, F, K, MICH, MO, NY); Nogales, *Matuda 1119* (A, MICH, MO, NY); Orizaba, *Botteri 227* (GH), *283* (GH). without precise locality: *Galeotti 2085* (F).

honduras: el paraiso: S of Güinope, *Williams 15762* (F, US). morazán: V. Guaimaca, *Molina 3143* (F, US); Mt Uyuca, *Carlson 2466* (F); *Molina 921* (F, GH), *Molina 10678* (US), *Williams & Molina 12619* (F). siguatepéque: above El Achote, *Yuncker et al. 6159* (F, GH). tegucigalpa: Montana de la Flor, *von Hagen & von Hagen 1293* (F, NY).

Saurauia willdemanii (see previous discussion of *S. pringlei*) was based on a Galeotti collection from Juquila, Oaxaca with the same number, *3088*, as the Jalapa, Vera Cruz collection. Buscalioni recognized the Hooker name, as well as two distinct varieties of *S. leucocarpa*, all based on Galeotti's Jalapa collection.

Its small flowers with completely glabrous sepals make *S. leucocarpa* one of the easiest species to identify.

21. Saurauia kegeliana Schlecht., Bot. Zeit. **11:** 694, 1853. (ex char.)

S. pauciserrata Hemsl., Diagn. Pl. Nov. 3, 1878. (Type: *Salvin s.n.*)
S. maxoni Donn. Sm., Bot. Gaz. **42:** 292, 1906. (Type: *Maxon & Harvey 3221*)

S. pauciserrata var. *kegeliana* (Schlecht.) Busc., Malpighia **25**: 13, 1912, nom. subnud. (Type: *Heyde & Lux 4328*)
S. pauciserrata f. *kegeliana* (Schlecht.) Busc., loc. cit. **29**: 7, 1921. (Type: *Heyde & Lux 4328*)
S. pauciserrata f. *crenata* Busc., loc. cit. 11. (Type: *Bernoulli & Cario 3347*)
S. pauciserrata f. *veranii* Busc., loc. cit. 22, nom. nud. (Type: *Salvin s.n.*)
S. intermedia Busc., loc. cit. 23. (Type: *Skinner s.n.*)

Shrubs and trees to 3-8 m; sparingly pubescent. *Leaf* blades obovate to narrowly elliptic, acuminate, the base subattenuate to acute, the margins crenulate or serrate to serrulate, 8-20 cm long, 2-8 cm wide, membranaceous to subcoriaceous, the secondary veins 7-11 pairs, the tertiary veins immersed, scarcely more prominent than the lesser reticulation, the veins scattered-tufted, the epidermis epustulate, glabrous except the villous-barbate axils of the secondary veins beneath; petioles 2-5 cm long, 1-2 mm in diam. *Inflorescences* 3- to 30-flowered, 5-16 cm long, 3-7 cm wide, the primary peduncle 2-11 cm long, scattered-tufted, the bracts linear to foliaceous, 1-25 mm long. *Flowers* 15-25 mm broad, buds to 4-5 mm in diam, the pedicels 3-25 mm long, abundantly to densely tufted, clustered and shaggy; sepals 5, margins ciliate, surfaces glabrous to densely appressed-stellate laterally without and within; petals 5, white, oblong to obovate, 6-14 mm long, 4-9 mm wide, obtuse to incised at the apex; stamens 24-28, the anther 2-3 mm long, the filament 2-4 mm long; ovary 5-locular, globose, 5-sulcate, glabrous, the styles 5, obsolete to 4 mm long, the stigmas subcapitate. *Berries* ca 10 mm in diam, globose, 5-sulcate, glabrous.

Dark forest, moist forest, wet mixed forest, second growth woods, opening in forest, wet thicket, brushy slope, south facing slopes, barranca, cleared area, along road; 550-3000 m; flowering from October to April.

Vernacular names: *Hoja de Níspero* (Guatemala—Aguilar), *Moquilla* (Guatemala—Standley); *Alais* (El Salvador—Padilla), *Capulín* (El Salvador—Carlson), *Capulín de Montaña* (El Salvador—Calderon), *Capulín Montes, Cerezo, Cresta de Gallo* (El Salvador—Standley).

MEXICO: CHIAPAS: Escuintla, *Matuda 16191* (F, NY); Mt Ovando, *Matuda 0482* (MICH, MO, US), *0575* (MICH, MO, US), *2654* (A, F, K, MICH, NY, US); Siltepec, *Matuda 5106* (F); V. Tacana, *Matuda 2975* (A, F, K, MICH, MO, NY).

GUATEMALA: ALTA VERAPAZ: vic of Secanquim, *Maxon & Harvey 3221* (US). AMATITLÁN: San Vicente Tadaya, *Tonduz 443* (US). BAJA VERAPAZ: nr San Geronimo, *Kellerman 6631* (F). CHIMALTENANGO: V. Acatenango, *Kellerman 6601* (F, US); Panajabal, *Standley 62130* (NY). GUATEMALA: Palencia, *Morales 938* (US); nr Finca La Aurora, *Aguilar 270* (F). QUEZALTENANGO: N of Colomba, *Holway 820* (US); ca 25 mi above Mazatenango on road to Quezaltenango, *Bunting 361* (MO); Palmar, *Skutch 1455* (A, NY, US); along Río Samalá, nr Santa María de Jesús, *Standley 84670* (US). SACATEPÉQUEZ: V. Acatenango, *Kellerman 4825* (F, US); V. Agua, *Standley 59508* (NY); above Dueñas, *Standley 63151* (A, NY, US); V. Fuego, *Salvin s.n.* (K), *Smith 1453* (GH, US). SAN MARCOS: betw Todos Santos & Finca El Porvenir, *Steyermark 37047* (F); betw Finca El Porvenir to "Numero 6" lower S-facing slopes of V. Tajumulco, *Steyermark 37141a* (F); above San Rafael Pié de la Cuesta, *Standley 68660* (F). SANTA ANA: NW flank of V. Santa Ana, *Tucker 1234* (NY, US). SANTA ROSA: nr El Molino, *Standley 60726* (F); El Teocinte, *Heyde & Lux 4328* (F, GH, NY, US). WITHOUT PRECISE LOCALITY: Barranca de Pinula, *Skinner s.n.* (K) *Bernoulli 266* (K), *285* (K); *Bernoulli & Cario 3347* (K); *Heyde 580* (US).

EL SALVADOR: AHUACHUAPÁN: Sierra de Apaneca, region of Finca Colima, *Standley 20065* (US); *Padilla 275* (US). LIBERTAD: Comasagua, *Calderón 1385* (GH, US); nr Comasagua, *Carlson 222* (F); nr Tecla, *Carlson 73* (A, US), *Standley 23069* (GH, US).

SANTA ANA: on Cerro de Los Naranjos, V. Santa Ana, *Williams et al. 15153* (F). SAN VICENTE: V. San Vicente, *Standley 21563* (GH, US). SONSONATE: San Juan de Dios, *Pittier 2002* (GH, US). WITHOUT PRECISE LOCALITY: V. San Salvador, *Calderón 447* (GH, US), *Standley 22933* (GH, NY, US).

The sepals of *S. kegeliana* show a clinal increase in the density of the pubescence of the sepals, from glabrous in the El Salvador collections to densely pubescent in the Mexican specimens. Sterile specimens are distinguished from *S. laevigata* by the villous-barbate axils of the secondary veins on the underside of the leaves and by the epustulate foliar epidermis.

22. SAURAUIA LAEVIGATA Triana & Planch., Ann. Sci. Nat., Sér. 4, Bot., **18:** 267, 1862. (Type: *Triana s.n.*)

S. yasicae Loes., Bot. Jahrb. **23:** 125, 1896. (Type: *Rothschuh 246*)
S. herbert-smithii Rusby, Descr. new sp. S. Amer. pl. 57, 1920. (Type: *H. H. Smith 857*)
S. leucocarpa Schlecht. var. *smithiana* Busc., Malpighia **29:** 232, 1922. (Type: *Türckheim 1445*)
S. yasicae var. *laevigata* Busc., loc. cit. (Type: *Tonduz 11453,* Donn. Sm. Pl. Guat. 7320)
S. yasicae var. *laevigata* f. *veranii* Busc., loc. cit. 413, 1923. (Type: *Tonduz 13147*)
S. smithiana Busc., loc. cit. 445. (Type: *H. H. Smith 857*)
S. pseudopittieri Busc., loc. cit. **30:** 97, 1927. (Type: *Pittier 11247,* Donn. Sm. Pl. Guat. 7318)
S. zetekiana Standl., Jour. Arnold Arb. **11:** 124, 1930. (Type: *Bangham 578*)
S. belizensis Lundell, Field & Lab. **13:** 7, 1945. (Type: *Gentle 4439*)

Trees to 30 m; sparingly pubescent. *Leaf* blades obovate to elliptic, obtuse to acuminate, the base subattenuate to obtuse, sometimes oblique, the margins serrulate to serrate, 6-22 cm long, 2-10 cm wide, membranaceous to chartaceous, the secondary veins 7-14, rarely 18 pairs, the tertiary veins immersed, scarcely more prominent than the lesser reticulation, the veins scattered-tufted, the epidermis pustulate, glabrous, not barbate in the axils of the secondary veins beneath; petioles 0.5-3.0 cm long, 0.5-2.5 mm in diam. *Inflorescences* 40- to more than 150-flowered 5-20 cm long, 2-10 cm wide, the primary peduncles 2-10 cm long, the bracts triangular to linear or foliaceous 1-35 mm long. *Flowers* 7-10 mm broad, buds 1-3 mm in diam, the pedicels to 1-6 mm long; sepals 4, rarely 3 or 5, 2-3 mm long, 2-3 mm wide, densely stellate laterally, becoming scattered-stellate to glabrous medially; petals 4, rarely 3 or 5, white, oblong to obovate, 4-5 mm long, 2-4 mm wide, obtuse to incised at the apex; stamens 20-30, the anther 1.0-1.5 mm long, the filament 1.5-2.5 mm long; ovary 4-, rarely 3- to 5-locular, globose, 4-, rarely 3- or 5-sulcate, glabrous, the styles 4, rarely 3 or 5, to 1 mm long at anthesis, the stigmas simple. *Berries* to 8 mm in diam, globose, 4-, rarely 3- or 5-sulcate, glabrous.

Virgin forest, deep forest, in coffee plantation with original forest trees, advanced forest, wooded valley, thicket along stream, stream bank, near river, slopes, in shade, hills, high ridge, edge of barranca; 30-1300 m; flowering throughout the year.

Vernacular names; *Jahoncillo, Wild Orange* (British Honduras—Gentle); *Chulindron* (Honduras—von Hagen).

MEXICO: CHIAPAS: Motozintla, *Matuda 16417* (NY); Mt Ovando, *Matuda 4171* (A, MO, MICH, NY); Palenque, *Matuda 3700* (A, MO, NY); Vieja, *Matuda 2526* (A, K, MICH,

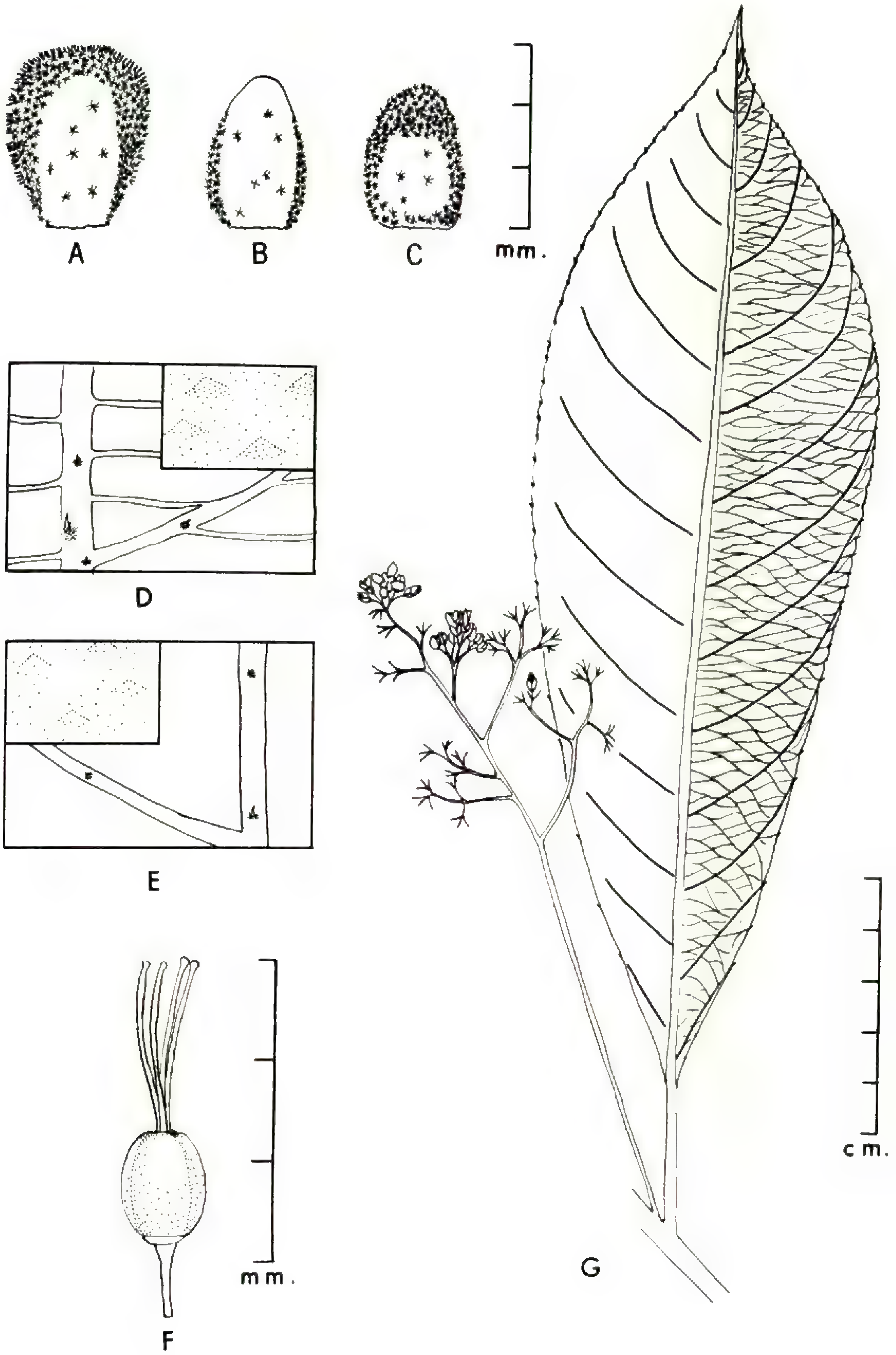


Fig. 5. *S. laevigata.* A. Inner sepal, outer surface; B. Outer sepal, outer surface; C. Outer sepal, inner surface; D. Lower leaf surface (inset—pustulate epidermis); E. Upper leaf surface (inset—pustulate epidermis); F. Ovary; G. Leaf and inflorescence.

NY). OAXACA: Santo Domingo, *Nelson 2672* (GH, US). TABASCO: Tenosique, *Matuda 3453* (A, MO, NY), *3555* (A, NY).

British Honduras: CAYO: El Cayo, Chalillo crossing, *Lundell 6519* (F, NY); Valentin, *Lundell 6185* (F, NY, US). STANN CREEK: Humming Bird Hwy, *Gentle 8254* (US), *8907* (US); Middlesex, *Gentle 2776* (A, F, NY, US), *2910* (A, F, MICH, NY), *2930* (A, F, NY), *3035* (A, F, MO, NY), *Schipp 236* (A, F, GH, MO, NY, US); Stann Creek Railway, *Gentle 2112* (A, F, MO, NY, US); Stann Creek Valley, *Stevenson 13* (US); Stann Creek Valley, Big Eddy Ridge, *Gentle 3352* (A, F, NY, US). TOLEDO: Punta Gorda, *Schipp 1003* (A, F, MO, NY).

Guatemala: ALTA VERAPAZ: Cobán, *H. Johnson 519* (US); Pansamalá, *Türckheim 1445* (GH, NY, US); Sacolol, *Türckheim II1892* (F, US). PETÉN: N of El Cambio, *Steyermark 45977* (F, US). QUEZALTENANGO: Colomba, *Skutch 1335* (A, F, NY, US), *1364* (A, F, US), *1987* (A, F, NY, US). RETALHULEU: San Felipe, *Smith 1493* (GH, NY, US); E of Santa Cruz Muluá, *Standley 88242* (F). SUCHITEPEQUEZ: Río Sis, *Smith 1494* (US).

Honduras: ATLÁNTIDA: vic of La Ceiba, *Yuncker et al. 8530* (F, GH, MO, NY, US), *8717* (F, GH, MO, NY, US), *8837* (F, GH, MO, NY, US); Lancetilla, *Yuncker 4628* (MO); Tela, *Bangham 241* (A, F, US); nr Tela, *Standley 53094* (A, F, US). CORTÉS: *Molina 5530* (F), *5666* (F); Montaña de Río Piedra, *Molina 3564* (F, US); nr Lake Yojoa, *Williams & Molina 14563* (F). SANTA BARBARA: Sauce, *Williams & Molina 14522* (F, GH, MO). YORO: Subirana, *von Hagen & von Hagen 1101* (F, NY).

Nicaragua: MATAGALPA: Cañada, Yasica, *Rothschuh 246* (US).

Costa Rica: ALAJUELA: San Ramon, *Brenes 19243* (NY). CARTAGO: Tuis, *Pittier 11247*, Donn. Sm. Pl. Guat. 7318 (US), *Tonduz 8109* (US), *11452* (US), *11453*, Donn. Sm. Pl. Guat. 7320 (GH, US); Turrialba, *Pittier 11242* (US). LIMÓN: Guácimo, *Tonduz 14892* (K). PUNTARENAS: vic of Esquinas, *Allen 5699* (F, US); betw Golfo Dulce & Río Térraba, *Skutch 5386* (US). TILARÁN: Arenal, *Valerio 3* (US). WITHOUT PRECISE LOCALITY: Las Vueltas, Tucurrique, *Tonduz 13147* (F, US); San Pedro de la Calabaza, *Cooper 10846* (US); Santa Clara, *Cooper 10240* (US).

Panama: CANAL ZONE: Barro Colorado Island, *Bangham 578* (A, F). *Salvoza 998* (A). COCLÉ: El Valle de Antón, *Allen 3630* (MO, NY, US); *Seibert 429* (A, F, NY); N of El Valle, *Allen 2180* (GH, MO, US); betw Las Margaritas & El Valle, *Woodson et al. 1733* (MO, NY); trail to Las Minas, N of El Valle de Antón, *Allen 2464* (F, MO, NY, US), *3706* (MO); N rim of El Valle, *Allen 1895* (GH, MO, NY, US). PANAMÁ: Cerro Azul, *Dwyer 2051* (MO).

COLOMBIA: CUNDINAMARCA: NW of Bogotá, Charco, *Little 7370* (US). MAGDALENA: Santa Marta, *Smith 857* (MO, US), *1774* (MO, P, US). TOLIMA: Libano, *Pennell 3306* (US).

Saurauia laevigata is the only species occurring in North America which is known to occur also in South America. With its glabrous foliar epidermis and small tetramerous flowers, it is the most easily identified of all the American species of *Saurauia*. Buscalioni (1922-1927), who recognized seven different names for this population, never realized the taxonomic significance of the tetramery of the flower. *Saurauia pseudopittieri* was based on a plant which I believe is a hybrid between *S. laevigata* and *S. pittieri*. It is cited here, primarily because of the predominent tetramery of its flowers and the characteristic venation and pubescence of its leaves.

Imperfectly Known Taxa of Saurauia

1. *S. behnickiana* Busc., Malpighia **30:** 360, 1927.

   This species was described from inadequate material as a dubious species. I have not seen the type.
2. *S. conzattii* Busc. var. *arthuriana* Busc., Malpighia **30:** 430, 1927.

   I have not seen the type and am unable to make a decision from Buscalioni's brief description.
3. *S. costaricensis* Donn. Sm. var. *scabrida* Busc., Malpighia **30:** 240, 1927.

   This variety was proposed as a dubious taxon. I have not seen the type.

4. *S. dubia* Busc., Malpighia **30:** 229, 1927.

As the name implies, this was published as a dubious species. I have not seen the type.

5. *S. radlkoferi* Busc., Malpighia **27:** 6, 1916.

I have not seen the type specimen on which this species was based; however, a photograph of the type specimen, published by Buscalioni in Malpighia, leads me to suspect that it is synonymous with *S. oreophila.*

6. *S. villora* var. *straussiana* Busc., Malpighia **30:** 348, 1927.

"Villora" is obviously a misprint of "villosa." This, too, was published as a dubious taxon. I have not seen the type.

Literature Cited

Brown, E. G. S. 1935. The floral mechanism of *Saurauia subspinosa.* Anth. Trans. & Proc. Bot. Soc. Edinburgh **31:** 485-497.

Buscalioni, L., & G. Muscatello. 1912-1927. Studio monographico sulle specie Americane del gen. *Saurauia* Willd. Malpighia **24:** 381-412; **25:** 1-16, 105-118, 187-250, 389-436; **26:** 1-32, 97-144, 281-312, 389-420; **27:** 1-32, 131-158, 293-324, 487-502; **28:** 1-48, 107-138, 223-238, 315-330, 371-402, 473-448; **29:** 1-32, 97-112, 230-246, 319-366, 411-458; **30:** 35-444.

Chandler, M. E. J. 1925. The upper Eocene flora of Hordle, Hants. Monog. Palaeog. Soc. Lond.

Corner, E. J. H. 1925. Centrifugal stamens. Jour. Arnold Arb. **27:** 423-437.

Diels, L. 1922. Die Dilleniaceen von Papuasien. Engl. Bot. Jahrb. **57:** 441-459.

Erdtman, G. 1952. Pollen morphology and plant taxonomy. Angiosperms. Almqvist & Wiksell, Stockholm.

Gilg, E. 1893. *Dilleniaceae—Actinidioideae* und *Saurauiodeae, In* Engler & Prantl, Natürl. Pflanzenfam. III. **6:** 125-128.

———, & E. Werdermann. 1925. *Actinidiaceae, In* Engler & Prantl, Natürl. Pflanzenfam., ed. 2, **21:** 36-47.

Hollick, A. 1936. The Tertiary floras of Alaska. U. S. Geol. Surv. Prof. Paper 182.

Lanjouw, J., et al. 1961. International Code of Botanical Nomenclature. (*Regnum vegetabile* 23)

Langeron, M. 1900. Contribution a l'etude de la flore fossile de Sezanne. Soc. Hist. Nat. Autun Bull. **13:** 333-370.

Lechner, S. 1915. Anatomische Untersuchungen über die Gattungen *Actinidia, Saurauia, Clethra,* und *Clematoclethra* mit besonderer Berücksichtigung ihrer Stellung im System. Beih. Bot. Centralbl. **32**(Abt. 1): 431-467.

Macbride, J. F. 1956. Flora of Peru (*Actinidiaceae*). Field Mus. Publ. Bot. **13** (Part 3A): 677-686.

Matthews, J. R., & G. Taylor. 1927. The structure and development of the stamen in *Erica hirtiflora.* Trans. & Proc. Bot. Soc. Edinburgh **29:** 235-242.

Schnarf, K. 1924. Bemerkung zur Stellung der Gattung *Saurauia* im System. Sitzber. Akad. Wiss. Wien, Abt. I. **133:** 17-28.

Smith, A. C. 1941. Studies of Papuasian plants, IV. Jour. Arnold Arb. **22:** 497-528.

Standley, P. C., & J. A. Steyermark. 1947. Studies of Central American plants, VII. Field Mus. Publ. Bot. **23:** 193-266.

———. 1949. Flora of Guatemala (*Saurauiaceae*). Fieldiana Bot. **24**(6): 428-438.

Thomas, J. L. 1961. The genera of the *Cyrillaceae* and *Clethraceae* of the southeastern United States. Jour. Arnold Arb. **42:** 96-106.

Enumeration of Series and Species of Saurauia

I. Series Gymnogynae
1. *villosa* DC.
2. *pittieri* Donn. Sm.
3. *rubiformis* Vatke
4. *comitis-rossei* Schultes
5. *pustulata* G. E. Hunter

II. Series Gynotrichae
6. *veraguasensis* Seem.
7. *squamifructa* G. E. Hunter
8. *waldheimia* Busc.

III. Series Oreophilae
9. *scabrida* Hemsl.
10. *pringlei* Rose
11. *oreophila* Hemsl.
12. *zahlbruckneri* Busc.
13. *aspera* Turcz.
14. *selerorum* Busc.
15. *conzattii* Busc.
16. *pedunculata* Hook.
17. *serrata* DC.
18. *angustifolia* Turcz.

IV. Series Laevigatae
19. *seibertii* Standl.
20. *leucocarpa* Schlecht.
21. *kegeliana* Schlecht.
22. *laevigata* Triana & Planch.

INDEX OF LATIN NAMES

New taxa are in **boldface** type, all other taxa are in roman type; numbers in **boldface** type refer to descriptions, numbers in roman type refer to synonyms, numbers with dagger (†) refer to names incidentally mentioned.

Actinidia 55†, 56†
Apetelia 57
Blumia 57
Clematoclethra 56†
Clethra 56†
Clethraceae 47†, 56†
Coriaria cuneifolia 78
Davya 57; serrata 78; villosa 58
Dilleniaceae 47†
Draytonia 57; rubicunda 57
Erica 56†
Ericaceae 56†
Ericales 47†, 56†
Guttiferales 56†
Leucothea 57; serrata 78; villosa 58
Marumia 57; cauliflora 57
Obelanthera 57; melastomacea 57, 58
Overstratia 57
Paulaua 57; lanceolata 57
Reinwardtia 57; javanica 57
Saurauia 47-88† **57**; sect. Pleianthae 55†; ser. Barbigerae 63; ser. Basilatae 68; ser. Gymnogynae **58**; ser. Gynotrichae **58**, **63**; ser. Laevigatae **58**, 68, **80**; ser. Mesophyllae 68; ser. Oligotrichae 48†; ser. Oleophilae **58**, **68**; ser. Scabrae 58; ser. Strigosae 48†; ser. Villosae 68; angustifolia **80**; anispoda 80; aspera 55†, **73**, 74†, 79†, f. delessertiana 73, 74†; barbigera 71†, 82, f. veranii 82; behnickiana 86†; belizensis 84; brachybotrys 53†; buscalioniana 70; comitis-rossei **61**; conzattii 49†, 53†, **77**, var. arthuriana 86†; costaricensis 64, 65†, var. brachitricha 64, var. dolicotricha 64, var. scabrida 86†; cuchumatanensis 77; dubia 87†; engleriana 64; englesingii 73; excelsa 57†; fluviatilis 78; herbert-smithii 84; intermedia 83; kegeliana **82**, 84†; laevigata 48†, 49†, 54†, 55†, 57†, 60†, **84**, 86†; latipetala 71; leucocarpa 49†, 54†, **82**, var. angustifolia 80, var. anisopoda 80, var. smithiana 84 var. stenophylla 80, f. veranii 80, 82, var. wildemanii 82; matudai 77; maxoni 82; montana 64; nelsoni 69; obelanthera 58; oreophila **71**, 75†, f. genuina 71, f. rubra 71; ovalifolia 64; parviflora var. ghiesbreghtii 71, f. delessertiana 74†; pauciflora 71, var. ghiesbreghtii 71; pauciserrata 82, var. kegeliana 83., f. crenata 83, f. kegeliana 83, f. veranii 83; pedunculata **78**, 79†, var. fluviatilis 78, var. leucocarpa 78 f. veranii 78, var. pringleana 82, var. reticulata 78, var. strigillosa 78, f. veranii 78; perseifolia 73; pittieri **59**, 60†, 61†, 86†, f. veranii 59; polyantha 60; pringlei 53†, **70**, 71†, 79†, var. micrantha 70; pseudopeduncularis 58;

pseudopedunculata 78; pseudopittieri 59, 60†, 84, 86†, f. veranii 59; pseudopringlei 82, var. fluviatilis 78; pseudorubiformis 60, var. guatemalensis 60; pseudoscabrida 64; pseudovaraguensis 64, 65†; **pustulata 63**; radlkoferi 87; reticulata 78; roborans 55; rubiformis 49†, **60**, 61†, f. aspera 60, f. veranii 60; sarapiquensis 60; scabrida 48†, 55†, **69**, 75†, var. hemsleyana 69; seibertii 48†, 61†, **81**; selerorum 48†, 52†, **74**, 75†, var. pseudonelsoni 69; serrata **78**, 79†; setosa 64, 65†; smithiana 84; speluncicola 58; **squamifructa** 54†, **65**; subalpina 71, 75†; subspinosa 49†, 54†; tristyla 55†; veneficorum 48†, 67; veraguasensis 48†, 54†, **64**; villora var. straussiana 87†; villosa **58**, 75†, var. hahni 58, 59†, var. macrantha 69, var. scabrida 69, var. tuberculata 69; waldheimia 48†, 54†, **67**, 68†; wildemanii 70, 71†; willdenowii 71†; yasicae 84, var. laevigata 84, f. veranii 84; zahlbruckneri 53†, **72**; zetekiana 84.
Scapha 57
Synarrhena 57
Tonshia 57; polypetala 57
Trematanthera 57; dufaurii 57
Vanalphimia 57

TWO NEW SPECIES OF CHAMAESYCE (EUPHORBIACEAE), NEW COMBINATIONS, AND A KEY TO THE CARIBBEAN MEMBERS OF THE GENUS

BY DEREK BURCH

Missouri Botanical Garden and Department of Botany, Washington University, St. Louis, Missouri

ABSTRACT

Two new species of *Chamaesyce* S. F. Gray from Haiti are described, and a key provided to the genus in south Florida, the Bahamas, and the Greater and Lesser Antilles. Thirteen new combinations, eight of which involve a change of status, are also made.

The group of plants which includes those treated here as the genus *Chamaesyce* S. F. Gray has been differentiated from the remainder of *Euphorbia* L. s.l. in a rather uniform fashion, even by workers who would not allow it more than subgeneric status. Experience in the field corroborates this ease of separation, and, at least in the case of New World plants, there is no doubt whether or not an unknown belongs to the group.

Segregation as a distinct genus has been suggested by a number of workers, and adopted by the authors of several floras dealing with parts of the New World and Oceania. Croizat (1936) defends this by reference to the replacement of the aborted primary axis by secondary axes which he holds to be diagnostic, and also lists other characters shared by the group but which are not alone sufficient to give a discrete separation. His conclusions, and the status of several other segregates which have been proposed at various times, are at present under consideration at the Missouri Botanical Garden in a revision which will eventually extend to cover all New World members of the *Euphorbieae*.

The work completed to date on the genus in the Caribbean region showed the existence of considerable synonymy, as might be expected in a very plastic group with wide-ranging species which has been studied for the last hundred years mostly on an island-by-island basis. The area covered includes south Florida, the Bahamas, and the Greater and Lesser Antilles, but excludes the coast of Venezuela and its islands. It was thought that these limits represented boundaries of a floristic region, and, with the exception of a few species with ranges extending into South America, and some which are of Central American origin, the distribution of the taxa studied was limited to the area defined.

Publication in this abbreviated form was chosen in order to validate names used in annotations without the delay of finding journal space for a long revision, while still providing a key which will explain the annotations and allow the identification of field material.

My thanks are due to the Curators of the following herbaria for loan of specimens or for permission to use their facilities: A, BM, BUS, DUKE, E, F, FLAS, FSU, GH, IJ, K, LINN, MO, NCU, NSC, NY, PUR, UCWI, US, USF, W. Much

of the material summarised in this key was submitted as a dissertation entitled "A Taxonomic Revision of the Genus *Chamaesyce* (*Euphorbiaceae*) in the Caribbean" to the Graduate Council of the University of Florida in August 1965.

Key To The Caribbean Taxa

1a. Large, much-branched shrubs; stems to 2 cm diam at base, 2-6 m long.
- 2a. Leaves fleshy, subglobose or linear; branches crowded, two-ranked, usually ± prostrate; coastal rocks, islands of the southern Bahamas .... *C. vaginulata* (Griseb.) Millsp.
- 2b. Leaves membranous, ovate to ligulate; branching divaricate, erect; southern Bahamas, Puerto Rico and Lesser Antilles .... *C. articulata* (Aubl.) Britton

1b. Annual or perennial herbs, often woody at the base, or small shrubs, but stems rarely exceeding 1 cm diam at base or 1 m in length.
- 3a. Capsule glabrous.
  - 4a. Plants erect or ascending.
    - 5a. Leaf margins manifestly toothed or, if entire, leaves ligulate.
      - 6a. Stems several to many from the crown of a heavy rootstock, wiry, rarely more than 1 mm diam; sandy barrens, Cuba and New Providence Island, Bahamas .... *C. brittonii* (Millsp.) Millsp.
      - 6b. Stems few to several, stout, to 4 mm diam; rootstock scarcely thickened.
        - 7a. Cyathia few, borne singly or in groups of two or three; perennial; pinelands, mountains of northern Haiti .... *C. parciflora* (Urban) Burch
        - 7b. Cyathia many, grouped on short leafy laterals or in glomerules; annual or perennating.
          - 8a. Capsule less than 1.4 mm long; cyathia usually in peduncled leafless glomerules; seed wrinkled; common weed throughout area .... *C. hypericifolia* (L.) Millsp.
          - 8b. Capsule more than 1.6 mm long; cyathia on leafy laterals; seed with 2-4 lateral ridges on each face; a frequent weed in all parts of area except the Bahamas .... *C. hyssopifolia* (L.) Small
    - 5b. Leaf margins entire or obscurely toothed below apex; leaves never ligulate.
      - 9a. Leaves and young stems fleshy; stipules conspicuous, membranous, white, to 1 mm long; beaches throughout area .... *C. buxifolia* (Lam.) Small
      - 9b. Leaves membranous or coriaceous, young stems not fleshy; stipules inconspicuous, coriaceous, brown, ca 0.5 mm long.
        - 10a. Stipules densely white-ciliate on adaxial surface; leaf and young stem minutely white-papillose; glands dark; appendages obsolete.
          - 11a. Plant branching from crown of root and throughout length of stem; branches decumbent; whitelands, Turks and Caicos groups of the southern Bahamas .... *C. lecheoides* (Millsp.) Millsp. var. *wilsonii* (Millsp.) Burch
          - 11b. Plant with few stems from ground level, branching mostly in upper part of stem; branches erect, strict.
            - 12a. Leaves linear-ovate, much longer than wide, apex acute; rocky shores and scrub, southeastern Bahamas .... *C. lecheoides* (Millsp.) Millsp. var. *lecheoides*
            - 12b. Leaves ovate-elliptic, scarcely longer than wide, apex obtuse; whitelands and coastal

sands, Bahamas from Eleuthera south to Great Ragged Island ....*C. lecheoides* (Millsp.) Millsp. var. *exumensis* (Millsp.) Burch

10b. Stipules not ciliate; stem smooth, somewhat waxy, leaf surface with raised markings but not papillose; glands green or red; appendages minute to twice width of gland.

13a. Leaves ovate-elliptic, most nearly as wide as long, apex obtuse to rounded; usually rather sparingly branched; pinelands, Dade and Monroe counties, Florida ....*C. porteriana* Small var. *porteriana*

13b. Leaves linear-elliptic, all except the oldest much longer than wide, apex acute; freely branched, often strict and broomlike; pinelands, Lower Florida Keys *C. porteriana* Small var. *scoparia* (Small) Burch

4b. Plants prostrate to decumbent.

14a. Stems minute, threadlike; styles undivided at apex; capsule less than 0.7 mm long; Haiti ....*C. tumistyla* Burch

14b. Stems substantial; styles bifid for part of length; capsule more than 1 mm long.

15a. Stems wiry and stiff, rarely exceeding 0.5 mm diam, usually many from heavy rootstock.

16a. Leaf margins entire.

17a. Leaves deltoid, margin somewhat revolute; glands fleshy, appendages minute or obsolete; capsule deltoid or reniform; pinelands, Dade Co, Florida ....*C. deltoidea* (Engelm. ex Chapm.) Small subsp. *deltoidea* var. *deltoidea*

17b. Leaves orbicular to elliptic, plane; glands cupped, appendages prominent, to three times width of gland; capsule ovoid-ellipsoid; savannas, Cuba ....*C. camaguayensis* Millsp.

16b. Leaf margins serrate, at least in the basal leaves.

18a. All leaves serrate, most 4-8 mm long; plants usually decumbent; savannas, Cuba ....*C. torralbasii* (Urban) Millsp.

18b. Only basal leaves serrate, most 2-3 mm (rarely to 5 mm) long; plants usually forming a loose prostrate mat; sand and coastal rocks, Salt Key Bank and New Providence, Bahamas, Cuba ....*C. centunculoides* (H. B. K.) Millsp.

15b. Stem flexible rather than wiry, reaching 2-3 mm diam, few to several from rootstock.

19a. Leaves and stems pubescent; seed very strongly wedge-shaped in cross section; Cuba ..*C. paredonensis* Millsp.

19b. Leaves and stems glabrous; seed subequally 4-sided or terete in cross section.

20a. Seed terete or obscurely angled; stipules not united, or minutely so at base, deeply parted or laciniate.

21a. Leaves usually fleshy, size often widely different on main stem and laterals; seed 1.4-1.9 mm long; coastal sands Florida, Cuba and northern South America ......*C. ammannioides* (H. B. K.) Small

21b. Leaves not fleshy, all similar in size; seed 1-1.4 mm long; stabilised dunes, southern Florida ....*C. cumulicola* Small

20b. Seed angular; stipules joined, at least on upper or lower surface of tips of branches, apex fringed or entire, never laciniate.

22a. Stipules toothed at apex, white, prominent although only ca 0.5 mm long; seed smooth; glands brown or deep purple, appendages white; common weed, all parts of area except Florida and Bahamas; Central and South America ....*C. serpens* (H. B. K.) Small

22b. Stipules toothed or bifid almost to base, green or tan colored, inconspicuous although often more than 1 mm long; seed obscurely transversely ridged; glands greenish, appendages white, yellow or pink.

23a. Texture of all parts of plant subcoriaceous; stipules to 0.4 mm long; leaf and stem surface somewhat papillose; perennial from a thickened rootstock; Puerto Rico, Antigua ....*C. cowellii* Millsp.

23b. Texture rarely firmer than membranous; stipules often exceeding 1 mm; leaf and stem surface smooth; annual or perennating but rootstock not thickened; weed, particularly of coastal areas, Florida, Bahamas, Cuba, Jamaica and Cayman Islands, rare in Virgin Islands ....*C. blodgettii* (Engelm. ex Hitchc.) Small

3b. Capsule pubescent.

24a. Leaf margins manifestly serrate.

25a. Plants erect to ascending with one or few thick stems; roadside weed, Jamaica, Haiti, Puerto Rico; Central and South America ....*C. lasiocarpa* (Klotzsch) Arthur

25b. Plants prostrate to decumbent; stems several to many, rarely exceeding 2 mm diam.

26a. Cyathia solitary at leafy nodes, appearing clustered if on congested laterals, but not in peduncled glomerules.

27a. Appendages of glands subequal in size, often much reduced, or if two appendages much longer than other two, capsule not fully exserted, splitting one side of cyathium at maturity; glands subcircular, only slightly elongated transversely.

28a. Ovary and capsule pubescent only along the angles.

29a. Stem short-pubescent in lines at sides and sometimes on upper surface; seeds with deep transverse furrows; weed, throughout area ....*C. prostrata* (Ait.) Small

29b. Stem long-hirsute, at least in lines at sides; surface of seed rippled; weed, Cuba, Florida; Mexico and northern South America ....*C. leucantha* (Kl. & Gke.) Millsp.

28b. Ovary and capsule pubescent all over.

30a. Capsule not completely exserted, splitting side of cyathium at maturity; weed, often nr salt water, Florida and rest of area except Bahamas and Cuba; Central and South America ....*C. thymifolia* (L.) Millsp.

30b. Capsule completely exserted at maturity.
31a. Leaf margin deeply and coarsely incised, often ½-⅔ distance to midrib; stems wiry, scarcely reaching 1 mm diam, many from heavy rootstock; limestone rocks, Navassa Island nr Haiti ....*C. hepatica* (Urban & Ekman) Burch
31b. Leaf margin serrate; stems not wiry, usually at least 1 mm diam, few to several from annual or perennating unthickened rootstock.
32a. Stem deliquescent through dichotomous branching in upper part; leaf texture heavy; seed strongly wedge-shaped in cross section; roadsides, northern Haiti ....*C. helwigii* (Urban & Ekman) Burch
32b. Stem excurrent, forming only congested leafy laterals in upper part; leaf texture membranous; seed almost square in cross section; weed of Florida as far south as Dade Co. ....*C. maculata* (L.) Small
27b. Appendages of glands greatly unequal in size, one pair longer than the other pair; capsule fully exserted and nutant at maturity, often concealed by the longer appendages; glands enlarged to extend much of the distance around the rim of the cyathium.
33a. Stems long-pilose on upper surface; leaf apex acute; cyathia congested on short laterals; pineland, Dade and Monroe counties, Florida ....*C. conferta* Small
33b. Stems short-tomentose or strigose on upper surface; leaf apex obtuse or rounded; cyathia borne singly or in small groups at upper nodes, if on laterals not congested.
34a. Leaves usually 5-10 mm long; stems few, sparingly branched, usually ca 1 mm diam, often strongly decumbent; seed angular, faces flat with transverse ridges; pinelands, mountains of Hispaniola ....*C. adenoptera* (Bertol.) Small subsp. *adenoptera*
34b. Leaves rarely reaching 5 mm long; stems several to many, often branching freely in upper part, rarely exceeding 0.5 mm diam; seed plump, subangulate, faces marked with short transverse grooves.
35a. Stems several, internodes short, forming a compact plant; appendages of glands prominent, larger pair usually more than 1 mm long; pinelands or sand, Florida, Cuba, Hispaniola and Mona Island ....*C. adenoptera* (Bertol.) Small subsp. *pergamena* (Small) Burch
35b. Stems many, internodes often long, giving plant an open appearance; appendages of glands prominent but

larger pair usually less than 1 mm long; sand or coastal rock, Cuba ....*C. adenoptera* (Bertol.) Small subsp. *gundlachii* (Urban) Burch

26b. Cyathia in peduncled glomerules.

36a. Leaf margins crenate-dentate or roundly serrate, apex obtuse; weed, Bahamas, Cuba, Hispaniola, Puerto Rico; isolated collections from Antigua and Guadeloupe. ....*C. berteriana* (Balb.) Millsp.

36b. Leaf margins sharply serrate, apex acute.

37a. Cymules terminal and lateral on leafless peduncles; stem branching at base but only infrequently near tip; mostly robust, ascending, large-leaved plants; weed throughout area ....*C. hirta* (L.) Millsp.

37b. Cymules terminal and on leafy laterals; stem branching freely; mostly low, decumbent small-leaved plants; weed in all parts of area, but uncommon from southern end of Antillean chain ....*C. opthalmica* (Pers.) Burch

24b. Leaf margins entire or obscurely toothed.

38a. Plants strongly suffrutescent, erect or ascending, 0.3-1 m in height.

39a. Glands deep purple, appendages obsolete; coastal scrub and whitelands, northwestern islands of the Bahamas ....*C. cayensis* (Millsp.) Millsp.

39b. Glands yellow or green; appendages prominent.

40a. Shrub, branched from base; capsules more than 2 mm long; Blue Mountains of Jamaica ....*C. myrtillifolia* (L.) Millsp.

40b. Suffrutescent, base mostly unbranched; capsules 1.3-1.5 mm long; coastal scrub, Lower Florida Keys ....*C. porteriana* Small var. *keyensis* (Small) Burch

38b. Plants herbaceous, or, if woody at the base, of small stature, rarely reaching 3 dm tall.

41a. Branches pubescent only on upper surface.

42a. Stem cespitose, erect, usually less than 0.5 mm diam; upper surface of leaf glabrous; Cuba ....*C. minutula* (Boiss.) Burch

42b. Stems not cespitose, prostrate, usually ca 1 mm diam; scattered white hairs on upper surface of leaf; Guadeloupe ....*C. multinodis* (Urban) Millsp.

41b. Branches pubescent on all surfaces.

43a. Cyathia in groups of 2-5 at nodes; seed strongly wrinkled; Haiti ....*C. leonardii* Burch

43b. Cyathia solitary at nodes; seed smooth or with transverse ridges but not wrinkled.

44a. Plants robust; stems not wiry, 1-3 mm diam, to 3 dm long; leaves 4-9 mm long; pineland and coastal sand, Dade and Monroe counties, Florida ....*C. garberi* (Engelm. ex Chapm.) Small

44b. Plants delicate; stems wiry, scarcely reaching 1 mm diam or 2 dm long; leaves 2-5 mm long.

45a. Plants closely appressed forming a dense mat, sometimes becoming diffuse with age.

46a. Leaves much longer than wide; mats becoming diffuse with age; pinelands, Lower Florida Keys ....*C. deltoidea* (Engelm. ex Chapm.) Small subsp. *serpyllum* (Small) Burch

46b. Leaves about as long as wide; tight mat form maintained with age; pinelands, Dade Co, Florida .... *C. deltoidea* (Engelm. ex Chapm.) Small subsp. *deltoidea* var. *adhaerens* (Small) Burch

45b. Plants erect or decumbent, at most forming a loose mat.

47a. Stems almost unbranched, villous-hirsute, tips canescent; capsule reniform, sharply three-lobed, angles acute; pinelands, Dade Co, Florida ...... *C. pinetorum* Small

47b. Stem branched freely, particularly in upper part, sparsely or densely short-pilose, tips only rarely canescent; capsule ovoid, roundly lobed, angles obtuse; rocky or sandy coasts, Cuba, Haiti, Puerto Rico, Anagada .... *C. turpinii* (Boiss.) Millsp.

New Species

Chamaesyce **leonardii** Burch, sp. nov.

Herba annua; caules prostrati, haud radicantes, tomentosi. *Folia* opposita; lamina ovato-elliptica, obscure serrata, tomentosa, infra purpurea; petiolus ca 1 mm longus; stipulae connatae, profunde bifidae, strigosae. *Cyathia* solitaria vel in ramis nudis brevissimis 2-5 fasciculata; involucrum obconicum, 0.6 mm diam, strigosum; glandulae transverse ellipticae substipitataeque, appendicibus nullis. Flores ♂ 3-10; flores ♀ stylo bifido 0.4 mm longo. *Capsula* albido-strigosa, ovoidea, 3-sublobata, 1 mm longa, 1.2 mm lata; semina ovoidea, 4-angulata, 0.7 mm longa, 0.4 mm lata, cineracea, parietibus rugosis.

Annual; prostrate; fruiting when stems 2-3 cm long; stem to 0.5 mm diam at base, internodes to 5 mm; branches reduced to groups of cyathia, not rooting at nodes, tomentose on all surfaces, greenish-yellow suffused purple. *Leaves* membranous or of a heavier texture; blades ovate-elliptic, 5-8 × 2.5-4 mm, base oblique, subcordate or rounded, margin obscurely serrated, thickened, apex obtuse, midrib prominent on lower surface, both surfaces strigose or sparsely tomentose, upper surface glabrate, lower surface minutely papillose, green suffused purple; petiole ca 1 mm long; stipules joined at base, 0.3 mm long, deeply bifid, strigose. *Cyathia* in leafless clusters of 2-5 at nodes; peduncle 0.3 mm long, involucre obconical, to 0.6 mm diam at mouth, lobes equalling glands, deltoid, strigose on outside, densely ciliate within, glands transversely elliptic, 0.05 mm long, somewhat stipitate, appendages obsolete, fifth gland short, deltoid, sinus broad, shallow. *Staminate flowers* 3-10 per cyathium, androphores glabrous, to 0.6 mm long at maturity. *Pistillate flowers* with gynophore strigose, to 1 mm long at maturity, exserted, upright or nutant; calyx a triangular pad of tissue; ovary densely white-strigose; styles spreading, 0.4 mm long, joined at base, bifid for ½-⅔ length. *Capsule* densely white-strigose, broadly ovoid, 1 mm long, 1.2 mm wide at equator, broadly 3-lobed, angles rounded; seed ovoid, 0.7 mm long, 0.4 mm wide, strongly angled, ventral angle rounded, faces convex, strongly wrinkled, red-brown or ashen, angles often lighter.

Type: Bluff E of Bord de Mer, vic of Jean Rabel, Haiti, 27 Jan-9 Feb 1929, *Leonard & Leonard 12888* (holotype NY, isotypes GH, K, US). Known only from type collection.

The cyathia of this species are borne in a manner not encountered in other species examined. The laterals near the tip of the stems are given over entirely to cyathia production, and consist of a group of one to a few cyathia congested on a stem a few millimeters long. This probably represents an extreme reduction of the type shown by *C. maculata* or *C. thymifolia*, in which cyathia are formed on congested leafy laterals in the upper part of the stem, rather than a further reduction from the glomerules of *C. berteriana* or *C. hirta*, since close observation shows that these cyathia alternate on the short stems, while in glomerules they fall at the nodes of a dichasium.

The white, strigose-pubescence of the capsules and the prominent midrib below the purple-flushed leaves are further distinctive features of the plant, and the wrinkled seed is also unusual.

No close affinities among species of the area are apparent for this species, but more mature plants may show features which suggest possible relationships.

The epithet *leonardii* was chosen in recognition of the contribution to the knowledge of the Haitian flora made by the extensive collections of Dr. E. C. Leonard.

Chamaesyce **tumistyla** Burch, sp. nov.

Herba annua; caules prostrati, usque ad 0.5 mm diam, nodis incrassatis, radicantes, supra strigosi. *Folia* opposita; lamina ovato-circularis, integra vel erosa, glabra; petiolus ca 0.3 mm longus; stipulae connatae, basi vaginulatae apiceque laciniatae. *Cyathia* solitaria, subsessilia; involucrum late campanulatum, 0.6 mm diam, glabrum; glandulae transverse ellipticae, crassae, appendicibus nullis. *Flores* ♂ 5-12; flores ♀ stylo indiviso 0.3 mm longo apiceque clavato. *Capsula* glabra, late ovoidea, 3-sublobata, 0.6 mm longa, 0.7 mm lata; semina ovoidea, 4-angulata, 0.4 mm longa, 0.2 mm lata, parietibus laevibus.

Annual or perennating; prostrate, forming mats to 2 dm diam; stem to 0.5 mm diam, internodes to 5 mm long; branched freely in upper part, rooting at nodes, nodes thickened, sparsely strigose on upper surface, glabrous beneath, light-colored. *Leaves* membranous, somewhat thickened, blades ovate-orbicular, 2-3 × 2-3 mm, base oblique, rounded or obtuse, margin entire or somewhat erose in drying, apex rounded, glabrous, green; petiole 0.3 mm long; stipules joined at base, sheathing, parted into linear segments 0.1 mm long. *Cyathia* solitary at upper nodes; sessile or minutely peduncled, broadly campanulate, to 0.6 mm diam at mouth, lobes scarcely equalling glands, deltoid, glabrous on outside, sparsely hairy within, glands transversely elliptic, fleshy, 0.3 mm long, appendages obsolete, fifth gland short, deltoid, sinus shallow. *Staminate flowers* 5-12 per cyathium, androphores glabrous, to 0.4 mm long. *Pistillate flowers* with gynophore glabrous, to 1.2 mm long, exserted, upright; calyx obsolete or a rim of tissue; ovary glabrous; styles upright or spreading, 0.3 mm long, joined at base, swollen at apex, undivided. *Capsule* glabrous, broadly ovoid, 0.6 mm long, 0.7 mm wide below equator, broadly 3-lobed, angles rounded;

seed ovoid, 0.4 mm long, 0.2 mm wide below equator, 4-angled, ventral angle sometimes obscure, others rounded, faces convex, plump, smooth, dark tan.

Type: Aviation field N of city, Mole St. Nicholas, Haiti, 13-19 Feb 1929, *Leonard & Leonard 13146* (holotype NY, isotype GH, US). Known only from the type collection.

There are marked differences between this tiny plant and any other species examined. The prostrate habit with stems rooting at the enlarged nodes is reminiscent of *C. serpens*, but the stems are tomentose on one surface, and are threadlike and much more slender than those of that glabrous species. The stipules differ, too, in being somewhat sheathing and yellow, rather than simply fused in pairs and white.

The subsessile cyathium has not been seen elsewhere, but the most distinctive feature is the undivided style swollen for the upper third of its length. No obvious affinities exist with other species of the area.

The epithet *tumistyla* refers to the enlarged apical portion of the undivided style and stigma.

New Combinations

Chamaesyce **helwigii** (Urban & Ekman) Burch, comb. nov., based on *Euphorbia helwigii* Urban & Ekman, Ark. Bot. **22**A(8): 65, 1929. Type: Road to Bassin, Les Gonaives, Presqu'île du Nordouest, Haiti, 24 Dec 1927, *Ekman H9546* (isotypes IJ, K, NY).

Chamaesyce **hepatica** (Urban & Ekman) Burch, comb. nov., based on *Euphorbia hepatica* Urban & Ekman, Ark. Bot. **22**A(17): 113, 1929. Type: Navassa Island, Haiti, 17-25 Oct 1928, *Ekman H10809* (isotype IJ).

Chamaesyce **minutula** (Boissier in DC.) Burch, comb. nov., based on *Euphorbia minutula* Boissier in DC., Prod. **15**(2): 1263, 1866. Type: Cuba, 1864-65. *Wright 2013* (isotypes GH, K).

Chamaesyce **opthalmica** (Pers.) Burch, comb. nov., based on *Euphorbia opthalmica* Pers., Syn. Pl. **2:** 13, 1807. Type: Rio de Janeiro, Brazil, July 1767, *Commerson 238* (holotype P-JU not seen, identity confirmed by Wheeler (1939) on basis of fragment in F).

Chamaesyce **parciflora** (Urban) Burch, comb. nov., based on *Euphorbia parciflora* Urban, Repert. Sp. Nov. **15:** 411, 1919. Type: Prope Marmelade, Haiti, 1-2 Aug 1905, *Nash & Taylor 1269* (isotype NY).

Chamaesyce adenoptera (Bertol.) Small subsp. **gundlachii** (Urban) Burch, comb. et stat. nov., based on *Euphorbia gundlachii* Urban, Symb. Ant. **5:** 392, 1908. Type: Cuba, 1865, *Wright s.n.* (not seen, B if extant).

Chamaesyce adenoptera (Bertol.) Small subsp. **pergamena** (Small) Burch, comb. et stat. nov., based on *Euphorbia pergamena* Small, Bull. Torrey Bot. Club **25:** 615, 1898. Type: Miami, Nov 1878, *Garber s.n.* (syntype NY); Lemon City, 2 Mar 1892, *Simpson 523* (syntype NY, dup. F, GH, US).

Chamaesyce deltoidea (Engelm. ex Chapm.) Small subsp. **serpyllum** (Small) Burch, comb. et stat. nov., based on *Chamaesyce serpyllum* Small, Fl. Florida Keys 81, 1913. Type: Big Pine Key, Monroe Co, Florida, 17 Nov 1912, *Small 3811* (holotype NY).

Chamaesyce deltoidea (Engelm. ex Chapm.) Small subsp. *deltoidea* var. **adhaerens** (Small) Burch, comb. et stat. nov., based on *Chamaesyce adhaerens* Small, Torreya **27:** 104, 1927. Type: Pinelands between Peters Prairie and Homestead, Florida, 10 Nov 1906, *Small & Carter 2531* (holotype NY).

Chamaesyce lecheoides (Millsp.) Millsp. var. **exumensis** (Millsp.) Burch, comb. et stat. nov., based on *Chamaesyce exumensis* Millsp., Field Mus. Nat. Hist., Bot. Ser. **2:** 301, 1909. Type: Stocking Island, Great Exuma, Bahamas, 22-28 Feb 1905, *Britton & Millspaugh 3071* (holotype F, isotype NY).

Chamaesyce lecheoides (Millsp.) Millsp. var. **wilsonii** (Millsp.) Burch, comb. et stat. nov., based on *Chamaesyce wilsonii* Millsp., Field Mus. Nat. Hist., Bot. Ser. **2:** 301, 1909. Type: Castle Island, Bahamas, 22 Dec 1907, *Wilson 7795* (holotype F, isotypes K, MO, NY).

Chamaesyce porteriana Small var. **keyensis** (Small) Burch, comb. et stat. nov., based on *Chamaesyce keyensis* Small, Torreya **28:** 6, 1928. Type: No Name Key, Monroe Co, Florida, 4-5 Feb 1916, *Small 7439* (holotype NY).

Chamaesyce porteriana Small var. **scoparia** (Small) Burch, comb. et stat. nov., based on *Chamaesyce scoparia* Small, Fl. Florida Keys 81, 1913. Type: Big Pine Key, Monroe Co, Florida, 17 Nov 1912, *Small 3819* (holotype NY).

Literature Cited

Croizat, L. 1936. *Chamaesyce* in Degener, Fl. Hawaii, family 190, *Chamaesyce* 1 & 4. Published by the author, Honolulu.

Wheeler, L. C. 1939. A miscellany of the New World *Euphorbiaceae*, II. Contr. Gray Herb. **127:** 48-78.

CHROMOSOME NUMBERS OF PHANEROGAMS. 1.

Chromosome numbers of phanerogams are reported below together with the voucher data and the herbaria where collections are deposited. Unless indicated the chromosomal records are based on the study of one plant. For haploid counts meiosis is regular unless otherwise noted.

The authors responsible for chromosome counts are listed alphabetically. Citation should have the form of: Doe, J. 1966. *In* Chromosome numbers of phanerogams. 1. Ann. Missouri Bot. Gard. **53:** pp.

BY WALTER H. LEWIS[1]

CONVOLVULACEAE

Calystegia sepium (L.) R. Br.: **n = 11.** Missouri: St. Louis, Missouri Botanical Garden, *Lewis 6638* (MO).

OROBANCHACEAE

Conopholis americana (L.) Wallr.: **n = 20 (±1).** Tennessee: Sullivan Co, between Bluff City & Bristol, *Lewis 6585* (MO).

PORTULACACEAE

Claytonia rosea Rydb.: **n = 8.** Colorado: Boulder Co, W side of Boulder, first Flat Iron, *Lewis 6642* (MO).

ROSACEAE

Rosa arkansana Porter: (1) **n = 14, 2n = 28.** Kansas: Bourbon Co, 1 mi S of Harding, *Lewis 2383* (MO); Cherokee Co, Turck, *Lewis 2377** (MO), 2 plants; Crawford Co, Girard to 8 mi N, *Lewis 2378** (MO); Linn Co, La Cygne, *Lewis 2386* (MO). Missouri: Clinton Co, Cameron to 6 mi S, *Lewis 2392** (MO), Wallace St Pk, *Lewis 2391** (MO). Meiotic abnormalities were found for collections from both Kansas and Missouri. For one plant of *Lewis 2377*, 20% of PMC had two chromosomes remaining in the equatorial region during telophase II and for a second plant examined at metaphase I two univalents were occasionally noted outside the equatorial area. Of the plants collected in Clinton County, Missouri, PMC with $13_{II} + 2_{I}$ were found (*Lewis 2391*) and, at diakinesis, with two interlocked ring bivalents (*Lewis 2392*).

Rosa arkansana Porter: (2) **2n = 30.** Kansas: Crawford Co, Girard to 8 mi N, *Lewis 2378* (MO). A rare aneuploid with an extra pair of chromosomes; another plant from the same collection is reported above with $2n = 28$.

Rosa arkansana Porter f. *plena* W. H. Lewis: **2n = 28.** Saskatchewan: Woodrow, *Lewis 2310* (MO, US).

Rosa blanda Ait.: **n = 7, 2n = 14.** Maine: Franklin Co, Farmington Falls, *Lewis 2504* (MO). New Hampshire: Coos Co, Jefferson, *Lewis 2172* (MO). New

[1] Aided by grant no. G-21818 from the National Science Foundation.

* Collections marked by an asterisk probably represent hybrid populations between *R. arkansana* and *R. carolina* L.

York: Onondaga Co, Green Lakes St Pk, *Lewis 2183* (MO). Ontario: Lanark Co, Blakeney, *Lewis 2448* (MO); Russell Co, 2 mi E of Clarence, *Lewis 2451* (MO). Quebec: Kamouraska Co, Kamouraska, *Lewis 2461* (MO); Rimouski Co, Bic, *Lewis 2466* (MO).

Rosa carolina L.: **n = 14, 2n = 28.** Georgia: Burke Co, Sardis to Alexander, *Lewis 2069* (MO); De Kalb Co, Stone Mt, *Lewis 2077* (MO); Morgan Co, Hard Labor Creek St Pk, *Lewis 2075* (MO), *Lewis 2076* (MO). Indiana: Martin Co, 2 mi S of Shoals, *Lewis 2411* (MO). Missouri: Daviess Co, Gallatin, *Lewis 2394* (MO), 2 plants; Oregon Co, 4 mi SE of Thomasville, *Lewis 2362* (MO); Ripley Co, Briar, Clark Natl Forest, *Lewis 2358* (MO); Sullivan Co, Milan, *Lewis 2398* (MO). New York: Cayuga Co, Cayuga, *Lewis 2186* (MO); Onondaga Co, Green Lakes St Pk, *Lewis 2180* (MO), *Lewis 2182* (MO); Sullivan Co, 2 mi N of Narrowsburg, *Lewis 2148* (MO). North Carolina: Burke Co, 3 mi NW of Morganton, *Lewis 2087* (MO). Ohio: Portage Co, Ravenna, *Lewis 2198* (MO). Pennsylvania: Lycoming Co, 1 mi W of Linden, *Lewis 2142* (MO). South Carolina: Sumter Co, Poinsett St Pk, *Lewis 2061* (MO). Virginia: Augusta Co, Mossey Creek, *Lewis 2427* (MO), West Augusta, *Lewis 2014* (MO); Highland Co, Lantz Mt, *Lewis 2018* (MO), 2 plants; Prince Edward Co, 2 mi S of Green Bay, *Lewis 2093* (MO); Prince William Co, Henry Hill, Bull Run Natl Battlefield Pk, *Lewis 2045* (MO), *Lewis 2049* (MO); Rappahannock Co, Hogwallow Flat Overlook, Shenandoah Natl Forest, *Lewis 2034* (MO), 1 mi S of Washington, *Lewis 2029* (MO); Shenandoah Co, Fort Valley, *Lewis 2438* (MO); Warren Co, 4 mi S of Front Royal, *Lewis 2032* (MO).

Rosa nitida Willd.: **2n = 14.** Quebec: Montmagny Co, Bertheir, *Lewis 2457* (MO).

Rosa palustris Marsh.: **n = 7, 2n = 14.** Illinois: Clay Co, Clay City, *Lewis 2407* (MO), Xenia, *Lewis 2406* (MO). Kentucky: Laurel Co, London, *Lewis 2337* (MO); Metcalfe Co, Wisdom, *Lewis 2341* (MO). Maryland: Garrett Co, Redhouse, *Lewis 2020* (MO). Missouri: Mississippi Co, 2 mi W of East Prairie, *Lewis 2349* (MO). New Hampshire: Cheshire Co, 7 mi N of Jaffrey, *Lewis 2156* (MO). North Carolina: Randolph Co, 5 mi S of Asheboro, *Lewis 2430* (MO). Ohio: Trumbull Co, Cortland, *Lewis 2197* (MO). Pennsylvania: Center Co, Bear Meadows, *Lewis 2136* (MO). Virginia: Gloucester Co, Gloucester Point, *Lewis 2002* (MO); Montgomery Co, 1.5 mi W of Blacksburg, *Lewis 2008* (MO); Norfolk Co, 2 mi S of Deep Creek, *Lewis 2022* (MO); Southampton Co, 2 mi W of Courtland, *Lewis 2026* (MO); Stafford Co, 11 mi NW of Fredericksburg, *Lewis 2436* (MO); Surrey Co, Spring Grove, *Lewis 2021* (MO). West Virginia: Nicholas Co, 5 mi E of Summersville, *Lewis 2422* (MO); Randolph Co, Cheat Mt, *Lewis 2019* (MO), 5 mi N of Valley Head, *Lewis 2425* (MO).

Rosa virginiana Mill.: **2n = 28.** New Brunswick: Carleton Co, Chancook, *Lewis 2501* (MO); Kings Co, Penosquis, *Lewis 2494* (MO).

Rosa woodsii Lindl.: **2n = 14.** British Columbia: Kamloops, *Lewis 2580* (MO). Saskatchewan: Moose Range, *Lewis 2308* (MO).

Rubiaceae

Anthospermum herbaceum L. f.: **n = 11.** Kenya: Rift Valley Prov, ENE slope of Mt Elgon, *Lewis 5959* (K,MO). South Africa: Transvaal, 24.8 mi SE of Barberton, *Lewis 6334* (K,MO), 2 plants.

Anthospermum littoreum L. Bolus.: **n = 11.** South Africa: Natal, Isipingo Beach, *Lewis 6290* (K,MO), 2 plants.

Borreria dibrachiata (Oliv.) K. Sch.: (1) **n = 28.** Tanzania: S Highlands Region, 5.3 mi E of Mbeya, *Lewis 6071* (K,MO).

Borreria dibrachiata (Oliv.) K. Sch.: (2) **n = 42.** Zambia: N Prov, 5 mi S of Abercorn, *Lewis 6104* (K,MO).

Borreria ocymoides (Burm. f.) DC.: **n = ca 14.** Kenya: Rift Valley Prov, ENE slope of Mt Elgon, *Lewis 5971* (K,MO), 2 plants.

Diodia natalensis (Hochst.) Garcia: **n = 14.** South Africa: Natal, 4 mi SE of Inyoni, *Lewis 6293* (K,MO), 2 plants.

Galium simense Fresen.: **2n = 44.** Kenya: Rift Valley Prov, ENE slope of Mt Elgon, *Lewis 5957* (K, MO).

Hedyotis galioides F. Muell.: **2n = 36.** Western Australia: Yule River, Woodstock Station, *Burbidge 5955* (AD), 2 progeny (*Lewis 6400*, K,MO).

Hedyotis michauxii Fosb.: **n = 16.** North Carolina: Cherokee Co, 2.2 mi SW of Cherokee-Swain Co line, *Lewis 6542* (MO).

Hedyotis purpurea (L.) T. & G.: **n = 12.** Missouri: Reynolds Co, top of Taum Sauk Mt, *Lewis 6443* (MO).

Hedyotis salzmannii (DC.) Steudel: **n = 15, 2n = 30.** Brazil: Guanabara State, Rio de Janeiro, *Lewis 6448* (MO), 2 plants. Meiosis is irregular in many PMC with univalents varying from two to six at metaphase I. About two-thirds of pollen grains were shrivelled.

Oldenlandia corymbosa L.: **2n = 18.** Brazil: Pernambuca Recite City, *Lewis 6445* (MO), 2 plants.

Otiophora cf. *caerulea* (Hiern) Bullock: **n = ca 18.** Zambia: NW Prov, 4 mi N of Kalene mission, *Lewis 6207* (K,MO).

Paederia scandens (Lour.) Merrill var. *mairei* (Lév.) Hara: **2n = 44.** Japan: N Honshu, Aobayama Botanical Garden, Sendai, *Lewis 6434* (MO).

Paraknoxia parviflora (Stapf ex Verdc.) Verdc. ex Bremek.: **n = 10.** Kenya: Rift Valley Prov, ENE slope of Mt Elgon, *Lewis 5954* (K,MO), *Lewis 5967* (K,MO).

Pavetta albertina S. Moore: **n = 11, 2n = 22.** Uganda: W Prov, Queen Elizabeth Natl Pk, *Lewis 6013* (K,MO), 2 plants.

Pavetta schumanniana F. Hoffm. ex K. Sch.: **n = 33.** Zambia: NW Prov, Mujileshi River, 4-5 mi E of Angola-Zambia border, *Lewis 6144* (K,MO).

Pentanisia angustifolia (Hochst.) Hochst.: **n = ca 20.** South Africa: Natal, Drakensberg Mts, base of Mt Champagne, *Lewis 6263* (K,MO).

Pentanisia confertifolia (Baker) Verdc.: **n = ca 10.** Zambia: N Prov, 3 mi S of Abercorn, *Lewis 6103* (K,MO).

Pentanisia foetida Verdc.: **n = 20.** Kenya: Central Prov, 2.7 mi E of Aberdare Natl Pk (eastern entrance), *Lewis 5926* (K,MO).

Pentanisia ouranogyne S. Moore: **n = 20.** Ethiopia: Harar Prov, 22.2 km S of junction of Harar-Giggiga Rd & Fich Rd, *Lewis 5864* (K,MO), 2 plants. Kenya: Rift Valley Prov, ENE slope of Mt Elgon, *Lewis 5965* (K,MO), 2 plants. Uganda: N Prov, 7 mi W of Namulu Prison, base of Mt Oboa, *Lewis 5989* (K, MO), 2 plants.

Pentanisia prunelloides (Kl. ex Eckl. & Zeyh.) Walp. subsp. *prunelloides*: **n = 20.** South Africa: Natal, Charters Creek, *Lewis 6295* (K,MO), 3 plants.

Pentanisia prunelloides (Kl. ex Eckl. & Zeyh.) Walp. subsp. *latifolia* (Hochst.) Verdc.: **n = 20.** South Africa: Natal, base of Mt Champagne, Drakensberg Mts, *Lewis 6263* (K,MO), 2 plants.

Pentanisia schweinfurthii Hiern: **n = 20.** Zambia: NW Prov, 1 mi SE of Solwezi, *Lewis 6130* (K,MO). Rhodesia: Salisbury Dist, Salisbury, Cranborne, *Lewis 6254* (K,MO). Tanzania: S Highlands Region, 5.3 mi E of Mbeya, *Lewis 6070* (K,MO), 2 plants.

Pentanisia sykesii Hutch.: **n = 20.** Zambia: S Prov, 8 mi SW of Choma, *Lewis 6242* (K,MO), 2 plants.

Psychotria nairobiensis Bremek.: **n = 11.** Kenya: Nairobi, Ainsworth Hill (cultivated), *Lewis 5907* (K,MO).

Richardia brasiliensis (Moq.) Gómez: **n = 14.** Brazil: Mato Grosso-Paraná States, Paraná River nr Guaíra, *Lewis 6444* (MO). Florida: Alachua Co, University of Florida campus, *Wiggins 19745* (DS, FLAS). South Africa: Natal, Charters Creek, *Lewis 6297* (K,MO), 2 plants.

Sabicea angolensis Wernh.: **n = 22.** Zambia: NW Prov, 4 mi N of Kalene mission, *Lewis 6195* (K,MO).

BY ROYCE L. OLIVER

IRIDACEAE

Sisyrinchium atlanticum Bicknell: **n = 16.** Florida: Hanes Co, 4.7 mi N of Bonifay, *Oliver 404* (MO), 3 plants. Mississippi: Jackson Co, intersection of Hwys 90 & 64, *Oliver 402* (MO).

Sisyrinchium cf. *atlanticum* Bicknell: **n= 8.** Georgia: Early Co, 2.5 mi NW of Early-Miller Co line & Hwy 39, *Oliver 452* (MO).

Sisyrinchium campestre Bicknell: **n = 16.** Iowa: Ringold Co, ca 2 mi N of Mount Ayr, *Lewis 6619* (MO).

Sisyrinchium demissum Greene: **n = 16.** Arizona: Greenlee Co, ca 77 mi N of Clifton, *Oliver 375* (MO).

NOTES

NEW SPECIES OF ALLOMARKGRAFIA AND ASPIDOSPERMA (APOCYNACEAE)

Allomarkgrafia **tubiflora** Woodson ex Dwyer, sp. nov.

Frutex scandens multiramosus, ramulis crassis teretibusque. *Folia* petiolis ad 1.5 cm longis; lamina oblongo-elliptica, apice abrupte acuminata basi obtusa vel rotundata, 7.3-11.5 cm longa, 2.1-4.3 cm lata, subcoriacea glabra. *Inflorescentiae* axillares proximis foliis breviores. *Flores* 2-7, albidi, pedicellis 0.7-2.0 cm longis; calyx lobis ovato-oblongis, apice gradatim rotundatis, 2 mm longis, glabris ciliatis; squamellae ∞ difformes ligulatae ad dentiformes; corolla infundibuliformis extus glaber venis lineatis, tubo tubuloso, 3.0-3.2 cm longo, ore ca 7.0 mm lato, lobis oblique obovatis, 1.0-1.4 cm longis, diffusis; antherae oblongae, basi cordatae, ca 5.0 mm longae, 2.0 mm latae; carpella oblongo-ovoidea, ca 2 mm longa, nectariis 5 apice oblongo-ovoideis gradatim rotundatis ovario vix brevioribus. *Fructus* folliculares lineares, 10-30 cm longi, ad 0.3 cm lati, seminibus ca 3-4 mm longis, coma pallido-flava, 1.5-1.7 cm longa.

PERU. HUÁNUCO: Palo de Acero, elev 950 m, *Woytkowski 7648* (holotype MO).

The specific name *tubiflora* was selected by Dr. Robert E. Woodson, Jr. because of the distinctive shape of the corolla throat. In the other species of the genus the throat is either campanulate or conic. The throat ranges in length from 3.0-3.2 cm long, somewhat longer than in all other species of *Allomarkgrafia*.

Aspidosperma **darienense** Woodson ex Dwyer, sp. nov.

Arbores ca 3-10 m altae, ramulis juvenilibus indistincte sordide floccoso-puberulis et mox glabratis, cortice fusco firmo et striato, haud evidenter lenticellato. *Folia* irregulariter disticha, petiolis crassiusculis, ca 5 mm longis; lamina tenuicoriacea obovato-oblonga, apice subcaudato-acuminata, basi inaequilateraliter obtusa, 10-18 cm longa, 2.5-5.5 cm lata, supra glabra olivacea nitens, subtus pallida et indistincte papillata, venis secundariis congestis et late ascendentibus. *Inflorescentiae* laterales extra-axillares inaequilateraliter 2- vel 3-plo dichotomae omnino minute ferrugineo-puberulae, pedunculis crassiusculis et petiolis foliorum subaequantibus. *Flores* sessiles fasciculati, bracteis dense imbricatis reniformibus, ca 1 mm longis vel minoribus; calyx laciniis dense imbricatis, subaequalibus suborbiculari-reniformibus obtusis, ca 1-1.5 mm longis, minute appresso-ferrugineo-puberulis ciliolatis eglandularibus; corolla (in alabastra bene evoluta) ut videtur tubuliformis vel tubuliformi-salveriformis, carnosa extus minuto-sericea, tubo ca 1.5 mm longo, ore late subcampanulato et haud constricto, lobis anguste sagittatis, ca 1 mm longis, in alabastro basi tubi corollae insertis; ovarium ca 1.5 mm longum stylo subaequale minute puberulum. *Fructus* ignoti.

PANAMA. DARIEN: lowland forest, betw Río Chucunaque & Río Canglon, *Sexton & Knight s.n.* (holotype MO).

The leaves of this species, particularly in their texture and close venation, are so reminiscent of the foliage of *A. megalocarpon* (series *Nobiles*) as to be confusing in sterile specimens. The inflorescences and flowers, even though prior to anthesis,

are obviously those of series *Nitida,* notwithstanding. Within this series *A. darienense* keys readily to the vicinity of *A. nitidum, A. auriculatum,* and *A. pichonianum,* because of its extra-axillary lateral inflorescences, but from all of these it differs radically by its large, closely veined leaves and sessile, fasciculate flowers.—*John D. Dwyer, Missouri Botanical Garden, St. Louis.*

A NEW SPECIES OF PLATYMISCIUM (LEGUMINOSAE) FROM PANAMA

Platymiscium **darienense** Dwyer, sp. nov.

Arbores mediocres, ramulis teretibus conspicue lenticellatis eis ultimis oppositis brevibus, ad 8 cm longis dense nodosis tortuosisque. *Folia* ad 30 cm longa, petiolulis gracilibus rigidis et glabris, ad 1 cm longis, in sicco nigris, petiolis ad 5 cm longis basi curvatis et vix tumescentibus, rhachidibus gracilibus rigidibus, ad 0.2 cm latis; foliola imparipinnata, jugis 5 oppositis, jugo inferiore evidenter minore; lamina oblonga, acuminata, ad 1 cm, acumine ultime obtuso, ad 14 cm longa, ad 7 cm lata, subcoriacea nitens glaberque, marginibus vix callosis, costa supra plana subtus distaliter prominula, venis secundariis primum argute ascendentibus tunc arcuate proxime margines dispositis; stipulae deciduae. *Flores* non visi. *Fructus* evidenter plano-compressi, falcato-oblongi, apice basique obtusi, ad 18 cm longi, ad 7 cm lati, coriacei margine unilateraliter ad 4 mm involuto sed vix crassiusculo, venis patulis prominulis irregulari-obliquis, area seminis fornicata, oblongo-rotunda, ad 7 cm longa, ad 5 cm lata, pedicello ca 1 cm longo.

PANAMA. DARIEN: Río Tucuti betw Tucuti & Río Uroganti, *Duke 5279* (holotype MO).

The only other species known from Panama is *P. pinnatum* (Jacq.) Dugand well distributed throughout Central and South America. To my knowledge the very large leaves and leaflets as well as the large fruit are unmatched in size by any other species of this small genus.—*John D. Dwyer, Missouri Botanical Garden, St. Louis.*

NEW SPECIES OF COUSSAREA, MACHAONIA, AND PSYCHOTRIA (RUBIACEAE) FROM PANAMA

Coussarea **villosula** Dwyer, sp. nov.

Arbores mediocres, ramulis teretibus et nodosis minute puberulis. *Folia* petiolis 1-4 cm longis, crassiusculis puberulis; lamina lanceolata, apice acuminata basi acuta, ad 20 cm longa, ad 8 cm lata, rigido-papyracea, supra glabra subtus sparse villosula et conspicue reticulata, marginibus vix revolutis, costa supra prominula, subtus versus petiolum plus prominente, venis secundariis ca 15, ca 1 cm distantibus, vix arcuatis; stipulae triangulares, ad 8 mm longae, hirsutae. *Inflorescentiae* terminales, 2-4 cm longae, ad 2.5 cm latae, dense sericeo-villosae, pedunculo gracili simplici ad 2-3 cm longo, cymulis 3-4 flores ferentibus; bracteae subulatae, ad 2 mm longae. *Flores* alabastris fusiformibus, ad 0.5 cm longis; calyx

subcampanulatus, ad 2.5 mm longus, ad 1.6 mm latus, dense appresso-villosus et carnosus, dentibus 5 minutis; corolla ad 3.2 mm longa, ca 1 mm lata, carnosa glabra, lobis 5 imbricatis, ca 1 mm longis, apice falcatis obtusisque; antherae subsessiles cuneatae; pistillum stylo lineari-oblongo, ad 1 mm longo, ca 0.25 mm lato, stigmatibus 2 minimis, ovulis 2 in sicco brunneis, septo gracillissimo disjunctis. *Fructus* non visi.

Panama. darien: Cerro Pirre, from Río Pirre S to El Real, 750-1030 m, *Duke 5338* (holotype MO).

The densely villose and compact inflorescence with spindle-shaped buds readily distinguishes the new species. It is closely related to *C. talamancana* Standley, known only from a collection in Bocas del Toro, Panama (*von Wedel 1098*), and from the type collected in Costa Rica. The flowers are white.

Machaonia **tysonii** Dwyer, sp. nov.

Suffrutices ad 8 m alti, ramulis teretibus et laevibus minute puberulis, ramulis ultimis 3-3.5 cm distantibus, angulo 70° ascendentibus, ramulis vel foliatis (sed versus apicem efoliatis) et apice acutis et minutis stipulis ornatis, vel omnino efoliatis et spinis munitis, spinis distichis teretibus laevibus glabris acutissimis, 1-3 cm longis, basi ca 0.2 cm latis, omnibus spinis unilateraliter certe regulariter brevioribus. *Folia* petiolis gracilibus ad 0.3 cm longis, puberulis; lamina subrotunda, apice vix acuminata, basi rotunda, ad 3 cm longa, rigido-papyracea, costa plana supra evanescente, subtus prominula, venis secundariis ca 6 (3 basalibus flabellatisque reliquis forte arcuatis) subtus prominulis solum in venis costaque minute albido-puberula, areolis praecipue subtus minute tessellatis; stipulae non visae. *Inflorescentiae* terminales paniculatae, folia superiora excedentes, ad 12 cm longae, ad 14 cm latae, pedunculis simplicibus, ad 12 cm longis, ramis inferioribus inflorescentiarum saepe arcuatis, ad 6 cm longis et ad medium simplicibus, oppositis, fasciculis florum evidenter terminalibus; bracteolae minute subulatae, ca 1 mm longae; bracteae lineari-ligulatae vel late lanceolatae, ad 1.5 cm longae. *Flores* albidi; calyx angusto-cylindricus, ca 3.5 mm longus, subcostatus, lobis oblongo-rotundis, ad 0.8 mm longis, obtusis, minute appresso-sericeis; corolla ad 3.5 mm longa, tenuicarnosa extus minute diffuso-puberula, tubo intus dense villoso, lobis tubo subaequalibus oblongo-rotundis; antherae supra orem tubi exsertae, oblongae, ca 0.65 mm longae, filamentis ca 1 mm longis; pistillum stylo ca 3.5 mm longo, ca 0.25 mm lato, stigmatibus 2, ca 0.5 mm longo, ovulis 2, loculis 2. *Fructus* non visi.

Panama. los santos: thicket nr man-made dam, main hwy, Monagre Beach, *Dwyer 5067* (holotype MO).

The new species is named in honor of Dr. Edwin Tyson of the U. S. Army Tropic Test Center, Fort Clayton, C.Z. and Florida State University. It is readily distinguished from all other species of *Machaonia* by its elongate distichous spines arranged biseriately.

Palicourea **lusinaturalis** Dwyer, sp. nov.

Arbores medicores, ramulis laevibus glabris. *Folia* petiolis ad 2 cm longis, ad 0.2 cm latis, minute puberulis; lamina oblongo-lanceolata, apice subdeltoidea vix acuminata basi acuta vel subobtusa, ad 22 cm longa, 9 cm lata, rigido-chartacea viridisque iam discolor, venis solum minute puberulis, minute papillata praecipue

subtus, costa supra prominula, subtus prominente, venis secundariis ca 15 arcuatis, venulis immersis patulis evanescentibus; stipulae compresso-rotundae, ad 5 mm longae et 10 mm latae, rigidae, marginibus fortasse integris. *Inflorescentiae* late cymoso-paniculatae, ad 20 cm longae et 25 cm latae, pedunculis terminalibus et hic tribus flabellate dispositis, minute puberulis, ad 12 cm longis, ramis oppositis, bene distantibus, inferioribus forte ascendentibus, 2-3 cm longis, ramis superioribus brevibus patulisque, cymulis terminalibus compactis; bracteae lineari-ligulatae, eis in ramis inferioribus ad 8 mm longis, persistentibus. *Flores* subsessiles, alabastris rectangularibus, ad 4 mm longis, apice truncatis; calyx lobis primum ascendentibus dein patulis, triangularibus, obtusis, glabris, ad 1 mm longis, laevibus quam tubo paullo longioribus; corolla ad 4.5 mm longa, ca 2.7 mm lata, tubo basi paullo dilatato, lobis 5 (-6), anthesi erectis, apice galeatis, ad 2 mm longis, tubo dense villoso ca 1 mm a basi; antherae 5(-6) lineari-oblongae, filamentis ad 1.2 mm longis; pistillum disco magno, stylo ad 3.5 mm longo, ad 0.1 mm lato, ad apicem crassiusculo, stigmatibus 2, patulis, obconicis, ca 0.5 mm longis, ovulis 2 basaliter affixis, septo crasso. *Fructus* non visi.

PANAMA. COLÓN: NW part Canal Zone, area W Limon Bay, Gatun Locks & Gatun Lake, Río Piña-Río Media divide, *Johnston 1807* (holotype MO).

This species originally distributed as the well-known *Psychotria hebeclada* DC., is assigned to *Palicourea* as a new species. Its large leaves and basally inflated corolla with upright lobes are suggestive of *Palicourea*, although the hairs within the corolla tube are somewhat above the base. The fact that the branches of the inflorescence in the dried state shows no evidence of the red or purple coloration, marking the vast majority of species of *Palicourea*, might favor placing the species in *Psychotria*. The two basally attached ovules with a thick septum between leaves no doubt of its position in the *Psychotrieae* and I cannot associate it with any other species of the tribe seen by me in herbaria.

The flowers are white.

Psychotria **cerroazulensis** Dwyer, sp. nov.

Arbores ad 30 m altae, ramulis nodosis tortuosisque, cortice dense ferrugineo-villosuloso. *Folia* petiolis ad 5 cm longis, crassiusculis; lamina late elliptica vel oblonga, saepe oblongo-rotundata, apice late cuneata, ultime vix acuminata, basi acuta, ad 15 cm longa et 9 cm lata, rigide chartacea minutissime foveolata glabra praeter minuta diffusa et albida grana, costa supra prominula, infra prominente, venis secundariis ca 12 prominulis, laxe arcuatis (eis mediis 0.8-2 cm distantibus); stipulae ad 6 cm longae. *Inflorescentiae* terminales, 7-9 cm longae, pedunculis crassis, ca 0.6 cm latis, plano-compressis, dense ferrugineo-puberulis, simplicibus, ad 1.5-2 cm longis, ramis inferioribus 2, oppositis 2-3.5 cm longis, ramis superioribus solum 2-3, crassis et alternis, floribus in globosis fasciculis ad 1.5 cm latis dispositis; bracteae bracteolaeque deciduae. *Flores* subsessiles; calyx late gibboso-campanulatus, ad 3 mm longus, apice ad 4 mm latus, lobis 5 (-6) triangularibus vel oblongo-rotundis, ca 1-2 mm longis et 1.5 mm latis, crasso-carnosis et dense ferrugineo-villosulis; petala tubo solum ad 0.6 mm longo, lobis anthesi reflexis, rectangulari-oblongis, apice obtusis, ca 3 mm longis, intus alte crasso-galeatis ad medium ciliatis, ciliis ∞ gracilibus, ad 1.8 mm longis; antherae oblongae, ca 1.7 mm longae,

in sicco nigrae filamentis plano-compressis, ad 0.9 mm longis, ca 0.3 mm latis; pistillum stylo ad 1.3 mm longo, stigmatibus 2, ca 0.8 mm longis, ovario evidenter disciferente, ovulis 2, basaliter affixis, septo crasso. *Fructus* non visi.

Panama. panama: Cerro Azul, 600 m, *Dwyer 2875* (holotype MO).

The inflorescence with a few stout ferrugineous-puberulent branches terminated by densely globular masses of sessile ebracteolate flowers is unlike the inflorescence of any Central American species of *Psychotria* which I have seen. It bears a slight resemblance to *P. brachiata Sw.* and *P. capitata Sw.*, although these species are marked by very conspicuous bracts and bracteoles.

Psychotria **quiinifolia** Dwyer, sp. nov.

Suffrutices mediocres, ramulis subteretibus, cortice rubescenti laeve et glabro. *Folia* petiolis ad 0.7 cm longis, alatis (lamina folii decurrente); lamina late elliptico-lanceolata, ad apicem subcuneata dein conspicue acuminata, ad 13 cm longa, ad 6 cm lata, rigido-chartacea, sordido-rubro-fusca, supra glabra, subtus glabrescens praeter pauca cilia subrigida praecipue in costa marginibusque, costa prominula, venis secundariis ca 15, prominulis, late arcuatis, venulis prominulis patulis; stipulae rectangulari-oblongae, obtusae, ad 1 cm longae, ad 0.4 cm latae in sicco rigido-papyraceae. *Inflorescentiae* terminales, glabrescentes et compactae, pedunculis ca 3 cm longis, flabellate dispositis, ramis paucis, brevibus, cymulis parvis. *Flores* subsessiles; calyx late urceolatus, glaber nitensque, ad 1 mm longus, lobis deficientibus, margine solum undulato; corolla ca 4.5 mm longa, in medio vix gibbosa, extus glabra carnosaque intus dense villosa, lobis 5 ovato-oblongis tubo aequalibus apice obtusis vix galeatis, anthesi reflexis; antherae sessiles, oblongae, ca 0.8 mm longae, 0.45 mm latae; pistillum stylo ad 4 mm longo, supra medium crassiusculo, ad 0.35 mm lato, stigmatibus 2, ca 0.3 mm longis, ovulis 2, septo crasso. *Fructus* non visi.

Panama. bocas del toro: Almirante, Changuinola Canal, *Blum 1402* (holotype MO).

The new species is similar to the well known *P. undata* Jacq. whose vegetative parts also tend to have a characteristic rubescence in the dry state, as well as rectangular oblong stipules and several minute glands surrounding the large ovarian disk. The new species, however, is obviously glabrescent with the leaves completely glabrous above and broader than in *P. undata*. The inflorescence is markedly glabrescent; the flowers are smaller and have a calycine cup which is glabrous and lacks distinct teeth.

The fancied resemblance of the leaves to those of *Quiina panamensis* Standley accounts for the specific name.

Psychotria **victoriae** Dwyer, sp. nov.

Suffrutices mediocres, caulibus laevibus, glabris nodosisque. *Folia* superioria 3-5 cm distantia, petiolis ad 4 cm longis, glabris; lamina oblongo-lanceolata, apice acuta basi attenue acuta, ad 30 cm longa et 6 cm lata, papyracea, glabra, areolis patulis et evanescentibus, marginibus regularibus, costa supra immersa, subtus ad 0.2 cm lata, venis secundariis prominulis ca 20, laxe arcuatis dein proxime marginem propinquas venas jugentibus, venis intermediis plus divergentibus sed mox evanescentibus; stipulae saepe persistentes, compresso-rotundatae, ad 2 mm longae, ad 10

mm latae, glabrae. *Inflorescentiae* cymoso-paniculatae, axillares, ad 9 cm longae, glabrae, pedunculis ad 5 cm longis, rhachidibus ramos late divergentes (inferiores ad 6 cm longos) ferentibus, bracteis triangularibus, ad 3 mm longis, ad 2 mm latis, reflexis, bracteolis deciduis. *Flores* albidi, alabastris apice clavatis paullo tubo corollae latioribus; calyx globoso-campanulatus, ad 1.8 mm longus, ad 2 mm latus, glaber, dentibus 5 minutis triangularibus, ad 0.3 mm longis, vel evanescentibus, area infra dentes pauci-verruculosa; corolla ad 7 mm longa, extus glaber intus proxime stamina villosulosa; antherae 5 oblongae, ca 1 mm longae, filamentis ad 0.7 mm longis, supra medium tubi affixis; pistillium stylo ad 4 mm longo, versus apicem vix crassiusculo, ramulis styli 2 oblongis, ad 0.6 mm longis, ovario 2-loculato, ovulis 2, obovato-oblongis, ca 0.5 mm longis, septo crasso. *Fructus* immaturi globosi glabri.

PANAMA. CHIRIQUÍ: woods Finca Collins, Boquete, elev 5000 ft, *Sr. M. Victoria Hayden 164* (holotype MO).

With its axillary pedunculate inflorescences and ascending narrowly lanceolate leaves bearing widely arcuate veins, the new species suggests several species of *Hoffmannia*, a genus well represented in the mountains of nearby Costa Rica. However the presence in *P. victoriae* of a biloculate ovary with two ovules basally attached and separated by a thick septum, places it in *Psychotria.* Two allied species (so far as the inflorescence pattern is concerned) are *P. uliginosa* Sw. and *P. macrophylla* Ruiz & Pav. The former is distinguished by its much wider leaves which consistently dry a characteristic tan beneath, and by its fasciculate flowers. *Psychotria macrophylla* has much larger inflorescences than *P. victoriae* and the leaf veins are stiffer.

The new species is named in honor of the collector, Sister M. Victoria Hayden. —*John D. Dwyer, Missouri Botanical Garden, St. Louis.*

HEDYOTIS NICOBARENSIS LEWIS, NOM. NOV. (RUBIACEAE)

Hedyotis **nicobarensis** W. H. Lewis, nom. nov., based on *Hedyotis wallichii* Kurz, Jour. Asiatic Soc. Beng. **45**(2): 136, 1876, non Walp. (Repert. **2:** 498, 1843); *Oldenlandia wallichii* (Kurz) Craib, Kew Bull. **1911:** 388, 1911 (superfluously made by Pitard, Fl. Gén. Indo-Chine **3:** 120, 1922); *Oldenlandia rosea* Ridley, Roy. Asiatic Soc., Jour. Str. Br. **59:** 110, 1911, non *Hedyotis rosea* Raf. (Fl. Ludov. 77, 1817); *Hedyotis galioides* Wall., Cat. no. 866, 1829, nom. nud., non F. Muell. (Fragm. **4:** 38, 1863).

The species is said by Kurz to be common among the grass heaths of Camorta Island of the Nicobar Islands in the eastern Indian Ocean. *Hedyotis nicobarensis* has also been collected in Burma (W. Gomez and W. P. Amherst) as reported under Wallich's Catalogue no. 866 and also from Borneo (Hook. f., Fl. Brit. Ind. **3:** 53, 1880), Indochina (Pitard, loc. cit.), Malaya including Singapore (Ridley, Fl. Malaya Pen. **2:** 54, 1923), and Thailand (Craib, Fl. Siam. Enum. **2:** 52, 1932). —*Walter H. Lewis, Missouri Botanical Garden, St. Louis.*

ARCYTOPHYLLUM LARICIFOLIUM (CAV.) LEWIS, COMB. NOV. (RUBIACEAE)

Arcytophyllum **laricifolium** (Cav.) W. H. Lewis, comb. nov., based on *Hedyotis laricifolia* Cav., Icon. **6:** 54, *t.* 575, *f. 1*, 1801. The type is from Chile, *Neé s.n.* (type MA, not seen; photo MO).—*Walter H. Lewis, Missouri Botanical Garden, St. Louis.*

CONVOLVULUS ROZYNSKII (STANDL.) LEWIS & OLIVER, COMB. NOV. (CONVOLVULACEAE)

Convolvulus **rozynskii** (Standl.) Lewis & Oliver, comb. nov., based on *Jacquemontia rozynskii* Standl., Field Mus. Nat. Hist., Bot. Ser. **11:** 172, 1936. Holotype: *von Rozynski* 46 (F), mountain slopes nr San Vicente, Tamaulipas, Mexico.

Through the courtesy of the Chicago Natural History Museum the holotype and *von Rozynski 46a* (from the same locality) of *J. rozynskii* have been examined. The paired stigmas of both plants are linear with no demarcation between the stigmatic areas and the style and as such they clearly resemble the stigmas known for *Convolvulus* (Lewis & Oliver, Ann. Missouri Bot. Gard. **52:** 217-222, 1965); they are not similar to the oblong or elliptic stigmas of *Jacquemontia* species. Unfortunately Standley (loc. cit.) failed to note the stigmas and so to equate the species with the correct genus. He made reference instead to the close relationship of *C. rozynskii* to *J. abutiloides* Benth., which superficially resembles our new combination, but differs as Standley outlined in leaf morphology, peduncle length and indumentum as well as by their stigmas as we have noted. Moreover, the pollen of *C. rozynskii* is 3-colpate and thereby characteristic of *Convolvulus* (Lewis & Oliver, loc. cit.), but differs strikingly from the (12-) 15- (18-) colpate pollen of *J. abutiloides* and *Jacquemontia* as a whole.

Roberty (Candollea **14:** 34, 1952) gives *C. rozynskii* as a synonym of *Montejacquia fusca* (Meissn.) Roberty. The latter is a typical species of *Jacquemontia* and has little in common with *C. rozynskii.*

Still a fourth genus is associated with this species. I. M. Johnston distributed specimens of *Stanford et al. 960* (9 km E of Palmillas, Tamaulipas, Mexico, MO) under a new, but to our knowledge, unpublished specific epithet of *Bonamia.* Apparently he mistook the long stigmas of *C. rozynskii* for the characteristic paired styles of *Bonamia.*—*Walter H. Lewis and Royce L. Oliver, Missouri Botanical Garden, St. Louis.*

TWO NEW SPECIES OF GLOEOSPERMUM (VIOLACEAE) FROM PANAMA

The small neotropical genus *Gloeospermum* Triana & Planchon is represented in Central America by the two species: *G. boreale* Morton (Field Mus. Nat. Hist., Bot. Ser. **9:** 309, 1940) (Honduras) and *G. diversipetalum* L. O. Williams (Ceiba

4: 273, 1955) (Costa Rica). The revision of the *Violaceae* for the Flora of Panama (supported by N.S.F. Grant GB-170) permits me to report, for the first time, the presence of the genus *Gloeospermum* in Panama, where it is represented by two new species: *G. ferrugineostictum* and *G. portobelense.*

Gloeospermum **ferrugineostictum** A. Robyns, sp. nov.

Arbor ca 4 m alta, ramulis teretibus glabris viridibus punctisque numerosis elongatis ferrugineis praeditis. *Folia* alterna, disticha, glabra, petiolo crasso supra subcanaliculato et usque ad 1 cm longo; lamina anguste elliptica, basi acuta, apice longe obtuseque acuminata, marginibus integris vel supra medium subcrenulatis, usque ad 20 cm longa et 7 cm lata, chartacea, in sicco discolor, subtus obscurior, nervatione praecipue infra prominenti, praecipue infra dense ferrugineo-punctata punctisque in venis elongatis. *Inflorescentiae* axillares, cymis paucifloris, bracteis inconspicue puberulis ciliolatisque. *Flores* actinomorphi, pedicello (fructiferi) usque ad 5 mm longo 2 mm supra basim articulato inconspicueque puberulo et dense ferrugineo-punctato; alabastra ovoidea; calyx quincuncialis, sepalis subcircularibus apice rotundatis ad obtusis inconspicue puberulis ciliolatisque dense ferrugineo-punctatis inaequalibus 2 externis ca 1.8 mm diam 2 internis ca 2.5 mm diam persistentibus; petala (immatura) ovata, obtusa, ca 3.5 mm longa, flava subcarnosaque, apicem versus ferrugineo-punctata; stamina vix 3 mm longa, filamentis latis appendicibusque dorsalibus erectis in tubum vix 0.5 mm longum connatis, tubi margine superiore libero, antheris ca 1 mm longis appendicibusque apicalibus tenuiter scariosis plus minusve ellipticis obtusis ad acutis leviter inaequalibus usque ad 1.5 mm longis et 0.5 mm latis; ovarium glabrum. *Fructus* baccatus, globosus, in vivo viridis, in sicco cinereus, stylo persistenti ornatus, ca 8 mm diam, glaber.

PANAMA. BOCAS DEL TORO: s. loc., *von Wedel 445* (holotype MO, isotype F).

This new species is easily distinguished from all other species of *Gloeospermum* by the numerous (elongate or not) ferruginous puncta on the branchlets, on the leaves (especially on the lower surface of the blade), on the pedicels, on the calyx outside, and on the outer surface of the petals (especially toward the apex). The inflorescences are at first dichasial, the lateral shoots developing into cincinni. The staminal tube is composed of the five dorsal appendages of the filaments which are connate; in this case, the appendages are slightly longer than the filaments and the upper margin of the tube is consequently free. According to the label on the type specimen, the fruit (when fresh) is "about one half inch long."

Gloeospermum **portobelense** A. Robyns, sp. nov.

Arbor 4 m alta, omnino glabra. *Folia* alternata, disticha, petiolo supra subcanaliculato 3-6 mm longo, stipulis anguste ovato-triangularibus 6 mm longis et 1.5 mm latis celeriter caducis; lamina anguste elliptica, basi rotundata, apice acuminata, marginibus integris subundulatisve, usque ad 13.5 cm longa et 5 cm lata, chartacea, nervatione praecipue infra prominenti. *Inflorescentiae* axillares, cincinnis paucifloris. *Flores* actinomorphi, pedicello usque ad 5 mm longo 1 mm supra basim articulato; alabastra ovoidea, ca 5 mm longa; calyx quincuncialis, sepalis late ad latissime ovatis obtusis inconspicue ciliolatis inaequalibus 2 externis ca 1.5 mm diam 2 internis ca 1.8 mm diam; petala imbricata, ovata, obtusa, ca 5.5 mm

longa et 2.5 mm lata, albida subcarnosaque; stamina ca 3.8-4 mm longa, filamentis latis appendicibusque dorsalibus erectis in tubum connatis, tubo irregulariter lobato ca 0.7-0.8 mm longo margineque superiore libero, antheris ca 1 mm longis, thecis basi leviter divergentibus apice appendiculatis appendicibusque tenuiter scariosis oblongis ad oblongo-ovatis obtusis integris ad inconspicue erosulis vix inaequalibus ca 2-2.5 mm longis et 0.5-0.6 mm latis; ovarium ca 1 mm longum, 1-loculatum, placentis 3 ovulisque numerosis; stylus ca 4 mm longus, apicem versus sensim angustior; stigma punctiforme. *Fructus* ignotus.

PANAMA. COLÓN: Portobelo, Las Cruces trail, *Ebinger 116* (holotype US, isotype MO).

Gloeospermum portobelense is very closely related to the type species of the genus, *G. sphaerocarpum* Triana & Planchon (Ann. Sci. Nat., Bot., sér. 4, **17:** 128-129, 1862) (Colombia, Amazonas in Brazil, northern Peru); from the Brazilian specimens which I have seen it can readily be separated by its longer apical appendages of the anthers: in *G. sphaerocarpum* the appendages are about as long as the anthers (cf Eichler in Mart., Fl. Bras. **13**(1): *t. 79(1)*, 1871; Melchior in Engler & Prantl, Nat. Pflanzenfam., ed. 2, **21:** *fig. 153,* 1925; personal observation on *Ducke 556* (MO) and *Krukoff 5164* (MO) from Brazil), while in *G. portobelense* the appendages are more than twice as long as the anthers.

A key which permits separating the Central American species of *Gloeospermum* follows.

Leaves and calyx densely ferruginous-punctate .... *G. ferrugineostictum*
Leaves and calyx epunctate.
  Sepals unequal in size, the 2 outer sepals smaller than the 2 inner ones, 1.2-1.8 mm in diam.
    Apical appendages of the anthers ca 1 mm long; outer sepals ca 1.2 mm in diam, inner ones ca 1.7 mm in diam; leaf blades with the margins remotely serrate .... *G. boreale*
    Apical appendages of the anthers ca 2-2.5 mm long; outer sepals ca 1.5 mm in diam, inner ones ca 1.8 mm in diam; leaf blades with the margins entire or subundulate .... *G. portobelense*
  Sepals equal in size, ca 3 mm in diam .... *G. diversipetalum*

—*André Robyns, Missouri Botanical Garden, St. Louis.*

BERNOULLIA OLIV., A GENUS OF BOMBACACEAE NEW TO PANAMA

The genus *Bernoullia* Oliv. (in Hook. f., Ic. Pl., ser. 3, **2:** 62, 1876), which is not mentioned in the Flora of Panama, Part VI, Family 116 *Bombacaceae* (Ann. Missouri Bot. Gard. **51:** 37-68, 1964), belongs to the tribe *Matisieae* and is characterized as follows: tree with compound-digitate leaves; flowers secund, in many-flowered unilateral racemes; calyx campanulate and shortly 5-lobed; staminal tube long-exserted, laterally cleft almost to the middle, antheriferous at the apex, the anthers 15-20, biseriate, sessile; ovary 5-locular, each locule with ∞ ovules, these biseriate; stigma 5-lobed; capsules large, ligneous, dehiscent at the apex, 5-celled; seeds 8-12 in each cell, broadly winged, the wings turned upwards at the base and downwards at the apex of each cell; endosperm scant.

Bernoullia can be inserted in the generic key of the *Bombacaceae* of the Flora of Panama (loc. cit. 38) as follows:

bb. Seeds broadly winged.
Flowers large (ca 16 cm long in *G. darienensis* Pittier); calyx tubiform, 2-3-lobulate; staminal tube closed nearly to the apex, the anthers 5, subsessile to long-stipitate, large, spirally-twisted, vermiform; staminodes sometimes present; capsule unilocular, loculicidally dehiscent ....5. *Gyranthera*
Flowers rather small (ca 2 cm long in *B. flammea* Oliv.); calyx campanulate and shortly 5-lobed; staminal tube laterally cleft almost to the middle, antheriferous at the apex, the anthers 15-20, biseriate, sessile, small, oblong; staminodes none; capsule 5-locular, dehiscent at the apex ....5a. *Bernoullia*

The genus, which consists of two or three species in Central America and in Colombia, is represented in Panama by the following species:

Bernoullia flammea Oliv. in Hook. f., Ic. Pl., ser. 3, **2:** 62, *t. 1169-1170,* 1876.

Mexico, Honduras, British Honduras, Guatemala, Panama, and northern Colombia.

CHIRIQUÍ: vic of Puerto Armuelles, fairly frequent in uncut areas of forest W of town, alt 30 m, tree 90-100 ft, flowers blood red, Nov 1952, *Allen 6650* (F).
—*André Robyns, Missouri Botanical Garden, St. Louis.*

THE PUBLICATION DATE OF THE GENUS COCHLOSPERMUM (COCHLOSPERMACEAE)

Rickett and Stafleu, in *Nomina generica conservanda et rejicienda spermatophytorum* (Taxon **8:** 313, 1959; see also International Code of Botanical Nomenclature, Regnum Vegetabile **23:** 286, 1961), cite the genus *Cochlospermum* as follows:

Cochlospermum Kunth ex A. P. Decandolle, Prodr. **1:** 527, Jan. 1824.

This genus was validly published about two years earlier by Kunth himself in Humboldt, Bonpland and Kunth, *Nova genera et species plantarum,* as a footnote. The correct citation should read:

Cochlospermum Kunth in H. B. K., Nov. Gen. Sp. Pl. **5:** 297, June 1822.

This generic name was published one month earlier as a *nomen nudum* by Kunth in his *Malvaceae, Büttneriaceae, Tiliaceae, . . .* (p. 6, 12 May 1822).

The combination under *Cochlospermum* of the type species, *C. gossypium* (L.) DC. (*Bombax gossypium* L.), dates, however, from A. P. de Candolle, loc. cit.—*André Robyns, Missouri Botanical Garden, St. Louis.*

PAVONIA (PELTAEA) TRINERVIS (PRESL) A. ROBYNS, COMB. NOV. (MALVACEAE)

Krapovickas and Cristóbal, in *Revision del género Peltaea* (*Malvaceae*) (Kurtziana **2:** 135-216, 1965), take up the genus *Peltaea* (Presl) Standley which was originally described by Presl as a section of the genus *Malachra* L. (Rel. Haenk. **2:** 125, 1836) and later elevated to generic rank by Standley (Contr. U. S. Nat. Herb.

18: 113, 1916). In my recent revision of the *Malvaceae* for the Flora of Panama (Ann. Missouri Bot. Gard. **52:** 497-578, 1966) I considered *Peltaea* as a section of the genus *Pavonia* Cav. (p. 528); this agrees with the opinion of many recent authors, among others Standley (Jour. Wash. Acad. Sci. **17:** 168, 1927; Contr. U. S. Nat. Herb. **27:** 255, 1928), Uittien (Rec. Trav. Bot. Néerl. **33:** 770-772, 1936), and Kearney (Amer. Midl. Nat. **46:** 107, 1951; Leafl. West. Bot. **7:** 122, 1954 & **8:** 225, 1958). It is, however, not my purpose to discuss here the generic delimitation within the genus *Pavonia* s.l., but only to call attention to the species *Pavonia sessiliflora* H. B. K. (*Peltaea sessiliflora* (H. B. K.) Standley). This species has been misinterpreted by many authors, among others Gürke (in Mart., Fl. Bras. **12** (3): 492, 1892), Standley (Contr. U. S. Nat. Herb. **18:** 113, 1916 & **27:** 255, 1928), Uittien (loc. cit. 772), Kearney (loc. cit., 1954 & 1958), and myself (loc. cit. 530), who described the mericarps as being glabrous. In fact, as pointed out by Krapovickas and Cristóbal (loc. cit. 174), these are "cubiertos de pelos simples, rígidos" (see also the original description, H. B. K., Nov. Gen. Sp. Pl. **5:** 287, 1822). The Panamanian collections, with glabrous mericarps, should rather be referred to *Pavonia* **trinervis** (Presl) A. Robyns, comb. nov.; *Malachra trinervis* Presl, Rel. Haenk. **2:** 126, 1835; *Peltaea trinervis* (Presl) Krap. & Crist., Kurtziana **2:** 168, 1965; *Pavonia sessiliflora* sensu A. Robyns, Ann. Missouri Bot. Gard. **52:** 530, 1966, non H. B. K. (Nov. Gen. Sp. Pl. **5:** 281, 1822).—*André Robyns, Missouri Botanical Garden, St. Louis.*

HIBISCUS LUTEUS (ROLFE) L. O. WILLIAMS & A. ROBYNS, COMB. NOV. (MALVACEAE)

In a recent paper A. Robyns (Ann. Missouri Bot. Gard. **52:** 176-181, 1965) called attention to the genus *Wercklea* Pittier & Standley and pointed out that the characters given by Pittier and Standley to separate this genus from *Hibiscus* L. do not in fact serve adequately to distinguish *Wercklea* from *Hibiscus*. Consequently he reduced *Wercklea* to synonymy and provided two new names: *H. rolfeanus* A. Robyns for *W. lutea* Rolfe and *H. wercklei* A. Robyns for *W. insignis* Pittier & Standley, because earlier homonyms existed.

The name *H. luteus* does indeed appear in the literature, but is not validly published; it is only cited as a synonym, "*H. luteus* Pavon in Hb. (ined.)," by Hochreutiner in his revision of the genus *Hibiscus* (Ann. Conserv. Jard. Bot. Genève **4:** 88, 1900) under *H. brasiliensis* L. var. *luteus* Hochr. The specific epithet *rolfeanus* is thus superfluous and the new combination should read: *Hibiscus* **luteus** (Rolfe) L. O. Williams & A. Robyns, comb. nov.; *Wercklea lutea* Rolfe, Kew Bull. **1921:** 118, 1921; *Hibiscus rolfeanus* A. Robyns, Ann. Missouri Bot. Gard. **52:** 177, 1965, nomen illegitimum.—*Louis O. Williams, Field Museum of Natural History, Chicago, Illinois and André Robyns, Missouri Botanical Garden, St. Louis.*

CONTENTS

A contribution to the ecology of *Pelagophycus*,
by BRUCE C. PARKER and JOHN BLECK ... 1- 16

A preliminary ultrastructural study of the freshwater red alga *Compsopogon*,
by H. WAYNE NICHOLS, JOHN E. RIDGWAY and HAROLD C. BOLD ... 17- 27

Two new species of *Daphniphyllum*,
by TSENG-CHIENG HUANG ... 28- 31

The Asian genus *Neanotis* nomen novum (*Anotis*) and allied taxa in the Americas (*Rubiaceae*),
by WALTER H. LEWIS ... 32- 46

Revision of Mexican and Central American *Saurauia* (*Dilleniaceae*),
by GORDON E. HUNTER ... 47- 89

Two new species of *Chamaesyce* (*Euphorbiaceae*), new combinations, and a key to the Caribbean members of the genus,
by DEREK BURCH ... 91- 99

Chromosome numbers of phanerogams. 1 ... 100-103

NOTES ... 104-114. New species of *Allomarkgrafia* and *Aspidosperma* (*Apocynaceae*) 104-105. A new species of *Platymiscium* (*Leguminosae*) from Panama 105. New species of *Coussarea*, *Machaonia*, and *Psychotria* (*Rubiaceae*) from Panama 105-109. *Hedyotis nicobarensis* Lewis, nom. nov. (*Rubiaceae*) 109. *Arcytophyllum laricifolium* (Cav.) Lewis, comb. nov. (*Rubiaceae*) 110. *Convolvulus rozynskii* (Standl.) Lewis & Oliver, comb. nov. (*Convolvulaceae*) 110. Two new species of *Gloeospermum* (*Violaceae*) from Panama 110-112. *Bernoullia* Oliv., a genus of *Bombacaceae* new to Panama 112-113. The publication date of the genus *Cochlospermum* (*Cochlospermaceae*) 113. *Pavonia* (*Peltaea*) *trinervis* (Presl) A. Robyns, comb. nov. (*Malvaceae*) 113-114. *Hibiscus luteus* (Rolfe) L. O. Williams & A. Robyns, comb. nov. (*Malvaceae*) 114.

Volume 53 1966 No. 2

Annals
of the
Missouri Botanical Garden

The previous issue of the ANNALS OF THE MISSOURI BOTANICAL GARDEN, Vol. 53, No. 1, pp. 1-114, was published on May 6, 1966.

PUBLISHED BY THE BOARD OF TRUSTEES OF THE MISSOURI BOTANICAL GARDEN
AND WASHINGTON UNIVERSITY PRESS
ST. LOUIS, MISSOURI 63110

Annals
of the
Missouri Botanical Garden

A journal containing scientific contributions from the Missouri Botanical Garden and the Department of Botany of Washington University in affiliation with the Missouri Botanical Garden.

EDITORIAL COMMITTEE

WALTER H. LEWIS, *Editor*
Missouri Botanical Garden & Washington University

DEREK BURCH, *Missouri Botanical Garden & Washington University*
JOHN D. DWYER, *Missouri Botanical Garden & St. Louis University*
ANDRÉ ROBYNS, *Missouri Botanical Garden & Washington University*
GEORGE B. VAN SCHAACK, *Missouri Botanical Garden*

Information

THE ANNALS OF THE MISSOURI BOTANICAL GARDEN appears three times during the calendar year. Three numbers totaling about 400 pages constitute a volume.

Beginning with Volume 53, 1966:

Subscription Price	$15.00 per volume
Single Numbers	5.50 each

Contents of previous issues of the ANNALS OF THE MISSOURI BOTANICAL GARDEN are listed in the Agricultural Index, published by the H. W. Wilson Company.

Beginning June 1, 1962 the Stechert-Hafner Service Agency, Inc., 31 East 10th St., New York 3, N. Y., became sole agent for the ANNALS OF THE MISSOURI BOTANICAL GARDEN. The Agency handles all subscriptions, all claims beginning with volume 50 (1963) and all requests for back issues. Out-of-print number will be reprinted as may be required.

Under the arrangement with the Stechert-Hafner Service Agency, the Agency handles also all purchases of any portion of the ANNALS subseries known as the "Flora of Panama."

All matters regarding exchange continue to be handled by the Missouri Botanical Garden as in the past.

Printed by the Eden Publishing House, St. Louis, Missouri, 63103.

Annals
of the
Missouri Botanical Garden

Vol. 53 | 1966 | No. 2

REVISION OF THE NORTH AND CENTRAL AMERICAN HEXANDROUS SPECIES OF ARISTOLOCHIA (ARISTOLOCHIACEAE)[1]

BY HOWARD W. PFEIFER[2]

Department of Botany, University of Connecticut, Storrs

ABSTRACT

A taxonomic revision of the North American species of *Aristolochia,* exclusive of the Mexican pentandrous group, is presented. A total of 58 species is enumerated with descriptions, illustrations, distribution maps and complete taxonomic synonymy; seven species are novelties.

Aristolochia has an estimated 450 species distributed mainly throughout the world tropics and subtropics. Geographic areas richest in endemic species are Brazil and the island of Hispaniola; the numbers of species decline sharply as one moves northward and very few are capable of withstanding freezing temperatures.

The present revision includes all of the native or introduced species of North and Central America except those with five stamens. These pentandrous species are chiefly natives of Mexico; a taxonomic revision for them is in preparation.

Aristolochia in the New World has not been taxonomically revised for 100 years. Duchartre presented the most recent comprehensive treatment in an account of *Aristolochiaceae* for de Candolle's "Prodromus" (Duchartre, 1864); he recognized 171 species in the genus. There is an outline account of the genus in the second

[1] Rewritten portion of a thesis submitted in partial fulfillment for the Doctor of Philosophy degree at Washington University in affiliation with the Missouri Botanical Garden in June, 1963.

[2] I wish to express appreciation for support to several agencies and institutions during the six years' preparation of this paper. They include the Research Foundation of Southern Illinois University, the Missouri Botanical Garden, the Research Foundation of the University of Connecticut and the National Science Foundation (Grant No. GB-2761).

I am also deeply grateful to the curators of the following herbaria who furnished specimens for study or who aided in other ways, namely A, BM, COL, DS, F, FI, G-DC, GH, K, LE, LINN, MEXU, MICH, MO, NCU, NY, P, S and US.

ANN. MISSOURI BOT. GARD. **53** (2): 115-196, 1966.

The previous issue of the ANNALS OF THE MISSOURI BOTANICAL GARDEN, Vol. **53,** No. 1, pp. 1-114, was published on May 6, 1966.

edition of "Die Natürlichen Pflanzenfamilien" (Schmidt, 1935), but it is incomplete because not all species are described and some subgeneric categories are named as "catch-alls" for species not fitting into the framework of Schmidt's classification. An account of the collections then in the Berlin herbarium was prepared by Klotzsch (1859). More recent contributions to the taxonomy of the genus are a revision of near-eastern species by Davis & Khan (1961), an account of Brazilian species by Hoehne (1927) and a short paper splitting the genus into several segregates after Rafinesque by Huber (1960).

Morphology

Typically species of *Aristolochia* are lianas of temperate and tropical forested areas. Some species are perennial herbs which sprawl over shrubs or along the ground. A few are shrubs, small trees or small upright perennial herbs.

The leaves frequently are heart-shaped with a deeply cordate or subhastate base; many species have heteromorphic foliage. While leaf shape is a valuable character for many species in a general sense, a wide variety of shapes may occur on a single stem. Examples of species with variable or unusual leaf outlines are *A. bilobata, A. gigantea, A. lindeniana, A. passifloraefolia, A. peltata, A. pentandra, A. maxima, A. panamensis, A. tigrina* and *A. trilobata.* The leaves range from thin, light-green membranes to those of gray-green, subcoriaceous texture.

The first prophyll of an axilliary branch in individuals of some species becomes enlarged concurrent with the subtending leaf on the main axis. These *pseudostipules* are similar in appearance to a pair of connate, clasping stipules. In a few species, they are reliable characters for identification purposes.

The indument of the leaves and other organs is similarly varied. In some Antillean species, the upper surface of the leaves may bear minute hamate hairs while the lower is glabrous. In others, the stems, petioles, leaves and flowers are hispid-strigose, but judging from field observations, pubescence varies with exposure, soil, water relationships, and possibly other factors.

Flowers are always solitary in leaf or bract axils; the leaves of the flowering branch may be sharply reduced and the flowers aggregated in a racemiform or monochasial fashion, as in *A. bilabiata* and *A. serpentaria.* Some of the woody tropical species have cauliflorous inflorescences appearing umbelliform due to the greatly shortened internodes of the flowering axis (e.g. *A. veraguensis).* The bracteolate peduncles of *A. grandiflora, A. macrophylla* and *A. serpentaria* possibly have developed through the loss of branches or additional flowers at those nodes.

The calyx tube is composed of three united sepals. Arising from the apex of the ovary the calyx expands into an ovoid, gibbous *utricle.* From the distal end of the utricle the *tube* narrows perceptibly, finally widening to form the more or less expanded *limb.* The calyx sometimes has two additional intussusceptive structures. At the juncture of the utricle and the tube, the *syrinx* projects asymmetrically into the utricle cavity; where the tube and the limb join, the projection is a circular flange, the *annulus* (Fig.1). The strongly zygomorphic calyx is unlike the other parts of the flower, which are actinomorphic. Calyx coloration may change drastically during the life of the flower; purple may fade to yellow, green areas

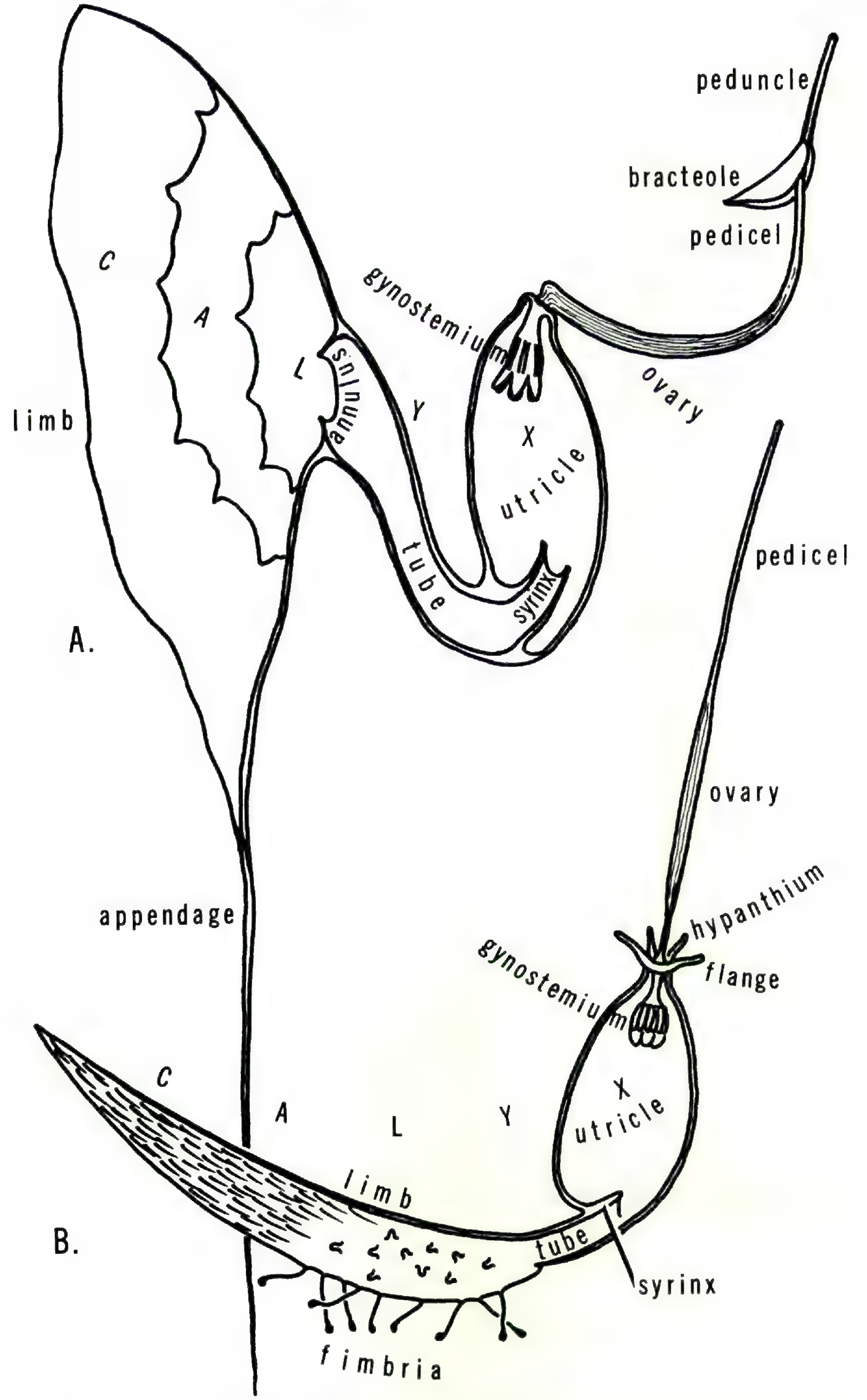


Fig. 1. Two hypothetical flowers illustrating the structures used in the keys and descriptions to define flower structure of *Aristolochia* in the present work; full discussion is in text.

may become translucent, and red spots or maculae may bleach and disappear. While it is generally true that the flowers may be described with regard to approximate color, no combination of colors in a description is an exclusive guarantee of accurate identification, especially in dried materials.

Illustrations of the various species which follow have not all been drawn to the same scale because of the broad range of floral size in the genus; however, the size of each is indicated by centimeter or, in the case of gynostemia, by millimeter scales. It has not been practical nor possible, in the several views presented of the flowers of some species, to make all of the drawings from the same flower; therefore, some allowance should be made for variation. Where gynostemia are illustrated, they cannot be assumed to be perfectly representative; they change during their ontogeny, particularly after the flower opens. Consequently, except for staminal number, they are comparatively less useful for identification than the details of the calyx and other features. Generally, the indument or pubescence of the flowers and leaves has been omitted in the drawings, but this is not critical, since variation is common and extreme. In any case, the descriptions are complete in this regard and should be referred to for details of the indument in any of the species.

Buds and mature flowers in many species of *Aristolochia* may be strikingly different and misleading in their proportions. This cannot be overemphasized. Furthermore, a merely "open" flower on an herbarium sheet may not necessarily be a mature one, since the flower buds are inflated during their ontogeny and always burst when the specimen is pressed; they split along the line of normal calyx valvate aestivation where the calyx is thinner and easily ruptured. The only true measure of maturity is the condition of the anthers and stigmas. These change sharply and significantly during the life of each flower and details of stigmatic structure and posture must be interpreted with the age of the flower borne in mind.

Another source of taxonomic error is the relative vigor of the flowers. Variation in size with true proportionality is common, but calyces with appendages also show great variation in the lengths of the latter. Flower size is influenced by the number of buds maturing on the branch; large numbers of buds produce uniformly small flowers while a single bud will develop into a large calyx. The dimensions of the gynostemium seem always to lie within comparatively narrow limits, whether the calyx tube is large or small.

An explanatory, schematic drawing (Fig. 1) elucidates some of the terms used in connection with the descriptions of the flowers; the upper flower, A, is geniculate and in the pistillate phase, the lower, B, is rectilinear and shedding pollen.

Lorch (1959) has presented interesting teratological evidence which suggests to him that the calyx of *Aristolochia* may be a greatly modified foliage leaf. This view is also held by Hagerup (1961) in studies on *A. elegans* (= *A. littoralis*).

Practically all of the West Indian species, as well as many others, have a rich covering of uniseriate hairs on the limb and in the tube. These wilt, become matted and generally are shed from the calyx following pollination; consequently

the limb and tube may be densely clothed in hairs or naked, depending upon the age of the flower. These hairs taper gradually along their whole length, ending in a fine, sharp point. Not to be confused with hairs are the curious *fimbriae.* These are enations found on the calyx limb of some species, which are fleshy, persistent, and often have a terminal, glandular swelling.

The styles, stigmas and anthers are closely united into a *gynostemium* which is usually a coroniform structure a few millimeters high. The sessile anthers are closely adnate to the lobes of the stylar column.

The gynostemium radically alters its outline and proportions during the ontogeny of the protogynous flower. The lobes, when young and approaching stigmatic maturity, generally are tall, thick and erect, greatly exceeding the tips of the immature anthers. Following pollination, the stigmatic lobes wither, bending inward upon themselves and exposing the turgid mature anthers. This sequence is illustrated in the drawing for *A. passifloraefolia* (Fig. 30).

I have noted in the field that following pollination the calyx and gynostemium of the large-flowered tropical species rapidly deliquesce. Old calyces are rarely found persistent at the tip of the fruit in any of the species. They are either autodigested similarly, or fall and decay quickly. This propensity for liquefaction can be frustrating when collecting these flowers in the humid tropics, where a specimen may be only a purple stain in newsprint after a few hours in an ordinary plant press; maggots, too, are fond of the damp flowers in a press.

Few tales of pollination wonders can surpass the sequence of events which lead to the production of seed in *Aristolochia.* The work of Petch (1924) is an exemplary account of extended investigation on this subject. I shall not attempt to review the innumerable accounts in the literature, but a summary of the events generally follows this succession:

1. *First day:* The stigmas are receptive—the tube hairs rigid, retrorse, allowing only entry of pollinators.

2. Pollination occurs through the agency of the insects imprisoned within the utricle.

3. *Second day:* the anthers dehisce, shedding pollen on the insects—the tube hairs wilt.

4. The insects leave, carrying pollen to another flower.

There are three reports known to me of presumptive cleistogamy in *Aristolochia serpentaria.* The oldest (1864) is a notation on a Leggett specimen, "with apet? flowers;" the second is the letter reproduced below. Both are taken from specimens deposited in the herbarium of the New York Botanical Garden.

"Dr. N. L. Britton: June 22, 1896
Dear Sir:

I send to you some plants of *Aristolochia Serpentaria* with what I think cleistogamous flowers. I've watched plants on a hillside near here and only once in 3 seasons have I found the ordinary blossom as described in Gray. This single instance was a few days ago. I've watched the plants from the time

the bud appeared till the fruit was nearly matured. I find no description of such a habit in this plant, & would like to ask if I am right in supposing it to be cleistogamous bloom and if it has been described before reporting it.

Respectfully,
Emma J. Thompson, M. D.
East Haddam, Conn."

The third report is a short note by Ahles (1959); he has generously collected special material for my study.

Flowers of *A. serpentaria* suspected of being self-pollinating (Fig. 4) have very small and rudimentary perianths. The calyx tube is reduced to a conic cover over the gynostemium, barely adequate to accommodate the enclosed structures. A short, oblique, gibbous tube is produced at the distal end of the calyx cone, its aperture being less than one millimeter in diameter and effectively plugged by the dense pilose hairs which clothe the whole flower. The gynostemium is somewhat aberrant when compared with that in a normal flower; there is, however, a full complement of six fertile anthers. The stigmatic lobes are unequally reduced; this is chiefly responsible for the abnormal appearance of the gynostemium. Material has not been available to allow an investigation of pollen tube growth or fertilization. The ovaries enlarge, but none of the specimens examined show conclusively whether the fruits present were produced from normal or cleistogamous flowers. The meager evidence suggests that either type may form fruit.

Resupination in the flowers of some species has been unreported by earlier investigators; there are several degrees of resupination in the species discussed here. Modification of floral structure is involved intrinsically with the twisting of the axis; the larger, median lobe of the calyx may be abaxial at anthesis (the normal state), or it may become adaxial by a 180° turn of the supporting axis. It may twist through several revolutions, making a numerical measure of the degree of resupination in the axis of the flower difficult. Since resupination is a response to gravitational pull of the symmetry of the flower, and *Aristolochia* flowers are strongly zygomorphic, there seems to be little point in establishing how many numerical degrees of revolution are produced; the effective rotation relative to the final posture of the flower is the significant point. As may be seen in Fig. 2, the flower bud emerges from the leaf axil with the median, largest calyx lobe in an abaxial position. This is modified by resupination in some species to the adaxial position; a very few species have an apparent double bend in the *floral axis*, which recreates the abaxial position of the median lobe. It is not clear whether the latter truly originates as a result of simple bending of the calyx or as a result of "double resupination," which would have the obvious effect of cancelling the resupination. It conceivably could be due to a combination of the two.

Since the utricle is *always* pendent from the apex of the ovary, this dictates the final posture of the flower. Thus, there is little difficulty in determining the position of the median lobe, enabling the flower to be described as resupinate (or geniculate) or rectilinear.

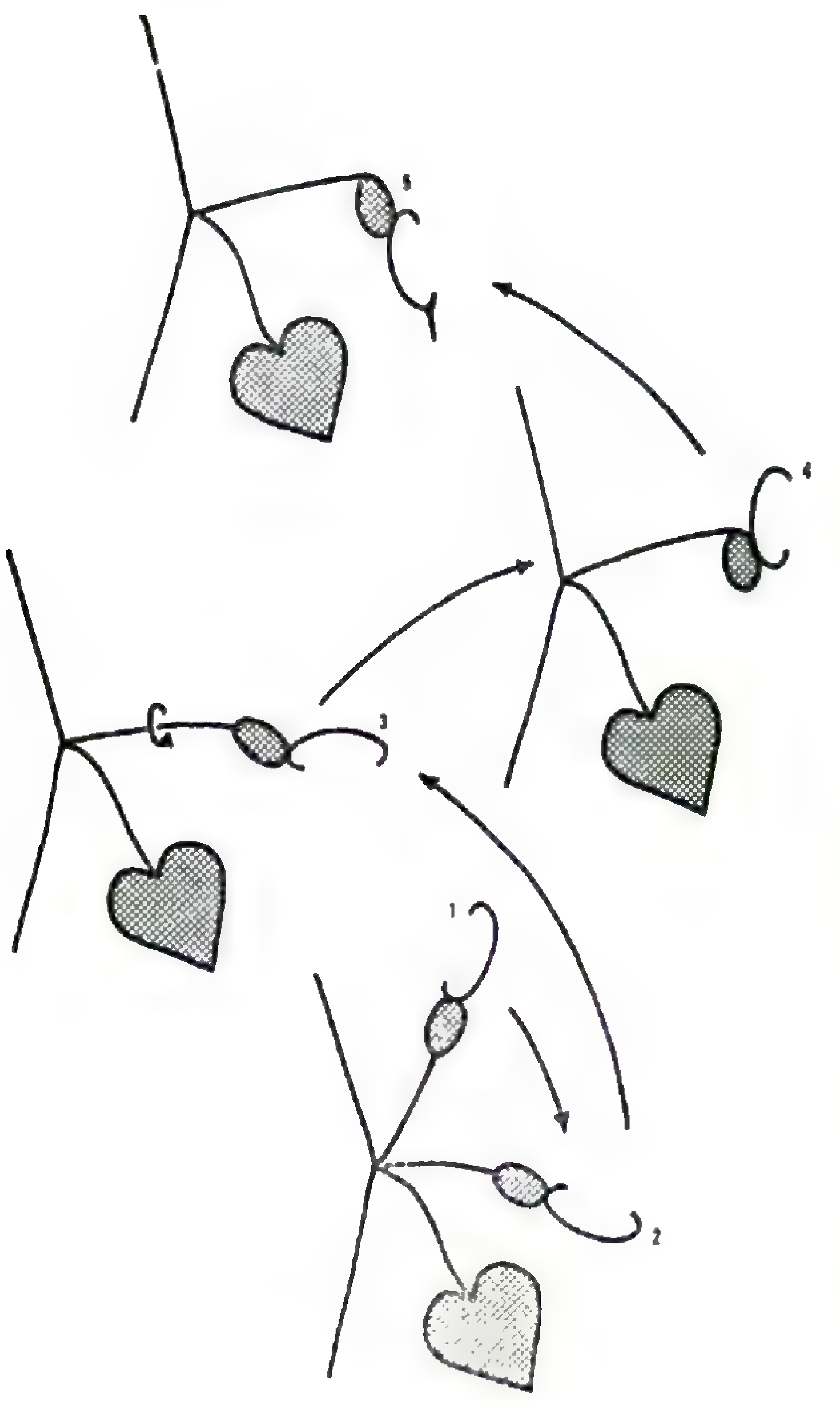


Fig. 2. Diagram representing floral resupination in *Aristolochia*. The stages shown, proceeding in the direction shown by the arrows, are: 1, the normal position of the flower in bud, with the largest medial calyx lobe abaxial; 2, a simple flexure in the peduncle of the flower allows the utricle to become pendent; then resupination rotates the flower, 3, into the commonest position for flowers in the species studied in this work; 4, the geniculate arching of the tube produces a further stage in which the limb is reflexed back upon the utricle, making the medial lobe of the calyx vertical and erect; 5, further resupination through a second flexure or a second rotation of the peduncle, produces a flower with the same configuration as in 2, but the flower is no longer rectilinear.

Human Uses

A few species of *Aristolochia* are widely used in horticulture. The large, strange flowers of *A. grandiflora, A. labiata* and *A. littoralis* are included in many greenhouse collections; *A. macrophylla* and *A. tomentosa* may be grown in temperate gardens, chiefly as arbor or trellis subjects.

The continuing search for plant derivatives which uniquely affect human disease and metabolism has led to the study of aristolochic acid. This substance, probably present in the tissues of many species, possesses the capacity to reduce growth of certain types of cancer in mice (Kupchan & Doskotch, 1962).

It is interesting to note that Rho Chi, an honorary pharmaceutical society in the United States, was known as the Aristolochite Society in its early history (ca 1908).

Aristolochia has an interesting etymology. Based upon the ancient usages dictated by the Doctrine of Signatures, and the fancied resemblance of the flower bud to the foetus, the plants were used as a source of medicine to alleviate the pain of childbirth. Thus, the name "best" (aristos) "delivery" (lochia) was coined.

Taxonomy

Aristolochia L., Sp. Pl. 960, 1753. (Type: *A. rotunda* L.)

Isotrema Raf., Amer. Monthly Mag. & Crit. Rev. **4:** 195, 1819. (Type: *I. sipho* (L'Herit.) Raf.)
Hocquartia Dum., Comm. Bot. 30, 1822. (Type: *H. macrophylla* (Lam.) Dumortier)
Dasyphonion Raf., First Cat. Bot. Gard. Transylv. Univ. 13, 1824. (Type: *D. tomentosum* (Sims) Raf.)
Cardiolochia Raf. ex Reichb., Consp. Regni Veg. 85, 1828, nom. nud.
Einomeia Raf., Medic. Fl. **1:** 62, 1828. (Type: *E. bracteata* Raf. = *A. pentandra* L.)
Endodeca Raf., loc. cit. (Type: *E. hastata* (Nutt.) Raf.)
Siphisia Raf., loc. cit. (Type: *S. glabra* Raf. = *A. sipho* L'Herit.)
Isiphia Raf., Medic Fl. **2:** 232, 1830. (Type: *I. glabra* Raf. = *A. sipho* L'Herit.)
Dictyanthes Raf. in Loudon, Gard. Mag. **8:** 247, 1832. (Type: *D. labiosa* (Edwards) Raf.)
Niphus Raf., loc. cit., nom. nud. = *Siphidia* Raf.
Siphidia Raf., loc. cit., nom. nud. = *Niphus* Raf.
Ambuya Raf., Fl. Tellur. **4:** 98, 1836. (Type: *A. labiosa* (Edwards) Raf.)
Diglosselis Raf., loc. cit. (Type: *D. trinervis* Raf. = *A. bilabiata* L.)
Hexaplectris Raf., loc. cit. 97. (Type: *H. bicolor* (L.) Raf.)
Plagistra Raf., loc. cit. 98. (Type: *P. cretica* (Lam.) Raf.)
Psophiza Raf., loc. cit. 99. (Type: *P. undulata* Raf. = *A. serpentaria* L.)
Pteriphis Raf., loc. cit. (Type: *P. tripteris* (Raf.) Raf.)
Tropexa Raf., loc. cit. 98. (Type: *T. biloba* (L.) Raf.)
Guaco Liebm., Forhandl. Skandin. Naturf. **1844:** 203, 1847. (Type: *G. mexicana* Liebm.)
Howardia Klotzsch, Monatsb. Acad. Berlin **1859:** 607, 1859, non Wedd. (1854). (Type: *H. ringens* (Vahl) Klotzsch)

Lianas, rarely upright perennial *herbs, shrubs* or *trees. Leaves* alternate, petiolate, estipulate but an axillary bud often producing a clasping, broadly reniform leaf (pseudostipule); blade entire or 2- to 7-lobed, often cordate, palmately or pinnately veined, often variable. *Flowers* axillary, solitary, perfect, epigynous, zygomorphic. *Calyx* gamosepalous, variously inflated, thence more or less contracted, ultimately expanding into a 1- to 3-lobed limb. *Corolla* absent. *Stamens* 5 or 6 or multiples of these, the anthers sessile and adnate to the style, 4-celled, dehiscing longitudinally. *Ovary* inferior, 5- or 6-loculate; placentation axile, the ovules numerous, anatropous. *Styles* 3, 5 or 6, marginally connate, fleshy, with coroniform to subcapitate stigmatic lobes. *Fruit* a capsule, dehiscence valvate or septifragal, acropetal or basipetal. *Seeds* usually numerous, more or less vertically compressed in 5 or 6 vertical rows, the embryo rudimentary in abundant endosperm.

Key[3]

1a. Calyx limb 3-lobed, without fimbriae.
  2a. Herbs of SE United States; flowers less than 2 cm long, in basal, bracteolate, racemose clusters.
    3a. Leaves isomorphic, elliptic-sagittate, subcoriaceous, strongly amplexicaul, the venation coarsely verrucose beneath .... 1. *A. reticulata*
    3b. Leaves heteromorphic, lanceolate to ovate, delicately membranaceous, the venation subimmersed beneath .... 2. *A. serpentaria*
  2b. Shrubs, trees or lianas, or if not woody, with tropical distributions.
    4a. Calyx lobes with linear, pendent appendages; leaves elliptic to oblong. Shrubs of Mexico & Guatemala.

[3] Including species of the United States, Mexico, the Central American Republics to and including Panama, the Greater and Lesser Antilles, the Bahamas and Bermuda.

5a. Flowers about 16 cm long; leaves acuminate, obtuse at the base, beneath tomentulose along the veins .... 3. *A. tricaudata*

5b. Flowers about 10 cm long; leaves obtuse at the apex, sagittate at the base, beneath woolly-tomentose .... 4. *A. malacophylla*

4b. Calyx lobes without appendages, acute, divergent; flowers 8 cm long or less.

6a. Calyx limb with a large inflated bulla or boss below the tube orifice. Mexico & Guatemala.

7a. Bulla capitate, stipitate; leaves oblong to elliptic; shrubs or small trees .... 5. *A. arborea*

7b. Bulla umbonate, sessile; (leaves unknown); lianas .... 6. *A. bullata*

6b. Calyx limb without a bulla.

8a. Leaves elliptic-ovate or orbiculate. Mexico & Central America.

9a. Utricle gradually contracted to an eccentric, tubular base.

10a. Syrinix a U-shaped thickening with the arms of the U extending and broadening onto the limb; leaves elliptic to suborbiculate, the apices obtuse. Lianas of Guatemala .... 7. *A. paracleta*

10b. Syrinx small, merely an inequilaterally annular flap; leaves ellipitic to ovate, the apices acute to acuminate. Shrubs of Panama .... 8. *A. panamensis*

9b. Utricle abruptly contracted at the base.

11a. Syrinx distinct, thick-walled, a constricted tubular passage into the utricular cavity.

12a. Leaves subsessile, auriculate, amplexicaul; syrinx urceolate. Shrubs of Mexico .... 9. *A. asclepiadifolia*

12b. Leaves short petiolate, slightly cordate; syrinx obliquely tubular. Shrubs of NE mexico ...... 10. *A. rhizantha*

11b. Syrinx absent, the throat of the flower wide open, not constricted or narrowed into a tube; leaves ellipitic-ovate, sagittate, shortly petiolate. Lianas of Nicaragua & Honduras .... 11. *A. thwaitesii*

8b. Leaves broadly cordate. United States.

13a. Peduncle bracteolate; calyx lobes concave, divergent; limb with a thin, inconspicuous faucal annulus.

14a. Plants glabrous to puberulent; flower with an obvious constricted tube between the utricle and limb. E United States .... 12. *A. macrophylla*

14b. Plants woolly to tomentose; flower without a constriction, the utricle apparently united directly with the limb. N California .... 13. *A. californica*

13b. Peduncle ebracteolate; calyx lobes convex, strongly revolute; limb with a prominent, rugose faucal annulus; plants tomentose. SE & south-central United States. .... 14. *A. tomentosa*

1b. Calyx limb 1- or 2-lobed.

15a. Leaves palmately 2- or 3-lobed; calyx limb without fimbriae; lianas.

16a. Calyx median lobe with a long, filiform appendage; flowers sharply geniculate; leaves large, 3-lobed. Caribbean islands, Central & South America .... 15. *A trilobata*

16b. Calyx median lobe without an appendage; flowers arcuate; leaves very small, 2-lobed. Hispaniola & St. Thomas .... 16. *A. bilobata*

15b. Leaves not palmately lobed.

17a. Leaves very strongly oblate-reniform.

18a. Calyx limb smooth, ovate, without fimbriae or warts. E Cuba .... 17. *A. lindeniana*

18b. Calyx limb fimbriate or warty.

19a. Flowers 7 cm long or more, the limb 6 cm long; leaves emarginate. Cuba, NE Hispaniola & St. Thomas .... 18. *A. peltata*

19b. Flowers 3 cm long or less, the limb 1.5 cm long.

20a. Leaves obtuse at the apex, apiculate, the base cordate. S Hispaniola .... 19. *A. leptosticta*

20b. Leaves emarginate, subrectangular, the base truncate. Gonave I. .... 20. *A. haitiensis*

17b. Leaves otherwise.

21a. Calyx limb fimbriate.

22a. Fimbriae few, long, chiefly marginal; limb broadly lanceolate, 2.5 cm wide; leaves cordate-orbiculate SW Mexico .... 21. *A. tentaculata*

22b. Fimbriae numerous, distributed over the surface of the limb; limb orbiculate, spatulate or sublinear, 2 cm wide or less.

23a. Plants hispid-pilose throughout; the limb lingulate-spatulate, sparsely to heavily fimbriate, fimbriae few, small; leaves ovate-triangular. S Mexico, Central & South America .... 22. *A. pilosa*

23b. Plants glabrous to glabrescent, not stiffly hairy.

24a. Leaves broadly cordate, not medially constricted; fimbriae variable, small and few to large and numerous. SW Mexico .... 23. *A. taliscana*

24b. Leaves broadly to narrowly pandurate, medially constricted.

25a. Fimbriae conspicuously capitate. Cuba.

26a. Fimbriae peltate-capitate; calyx limb ovate .... 24. *A. glandulosa*

26b. Fimbriae compressed-capitate; calyx limb spatulate .... 25. *A. clavidenia*

25b. Fimbriae subulate or only slightly swollen terminally.

27a. Calyx limb narrowly lingulate, emarginate, half the length of the calyx; fimbriae mostly marginal. Hispaniola .... 26. *A. fuertesii*

27b. Calyx limb broadly spatulate, less than half the length of the calyx; fimbriae distributed over the surface of the limb.

28a. Calyx limb 1.5-2.0 cm long, half as long as the tube. Lesser Antilles .... 27. *A. rugosa*

28b. Calyx limb 2-3 cm long, as long as the tube or longer. Cuba & the Bahamas .... 28. *A. passifloraefolia*

21b. Calyx limb without fimbriae.

29a. Calyx limb with 2 lobes, sub-equal in length, superposed one above the other, the lower narrowly lanceolate, often longer than the upper.

30a. Upper calyx lobe deflected, oblate-orbicular, narrowly clawed, ruffled. South America; escaped from cultivation in our area ....29. *A. labiata*

30b. Upper calyx lobe not deflected, obovate-spatulate. Circumcaribbean ....30. *A. ringens*

29b. Calyx limb 1-lobed, or if 2-lobed, the upper clearly longer than the lower.

31a. Calyx limb abruptly spreading from the tube, more than 6 cm wide.

32a. Leaves densely white-tomentulose beneath.

33a. Flowers 6 cm wide; leaves cordate at the base. Lianas. Location unknown ....31. *A. esoterica*

33b. Flowers 12 or more cm wide; leaves truncate at the base. Lianas of Panama ....32. *A. gigantea*

32b. Leaves glabrous.

34a. Flowers 10 cm wide, without an annulus.

35a. Hypanthium and utricle rectilinear from the ovary, pseudostipules present. Circumcaribbean. ....33. *A. littoralis*

35b. Hypanthium and utricle sharply deflected from the ovary, pseudostipules absent. Mexico, Central America, the West Indies & Florida ....34. *A. odoratissima*

34b. Flowers 20 to 50 cm wide, with an annulus; pseudostipules absent. Mexico, Central America & the West Indies. ....35. *A. grandiflora*

31b. Calyx limb gradually expanding from the tube, less than 5 cm wide.

36a. Leaves oblong, 3 cm long or less; flower axis about 5 cm long.

37a. Leaves with 5 basal veins, shallowly cordate; flowers extremely arcuate. Hispaniola ....36. *A. ekmanii*

37b. Leaves with 3 basal veins, subtruncate; flowers slightly arcuate. Cuba ....37. *A. tigrina*

36b. Leaves othewise, mostly much more than 3 cm long; flower axis more than 5 cm long (except *samanensis*, *clematitis* and *constricta*).

38a. Leaf bases cuneate, obtuse, truncate or shallowly cordate.

39a. Tube shorter than the utricle.

40a. Leaf undersurfaces prominently glaucous, smooth; flower axis about 2.5 cm long. Hispaniola ....38. *A. samanensis*

40b. Leaf undersurfaces green with prominent, raised, reticulate venation; flower axis about 10 cm long. Florida, Mexico, Central America & Martinique ....39. *A. maxima*

39b. Tube longer than the utricule.

41a. Pseudostipules absent.

42a. Leaves smooth, with immersed venation, narrowly triangular, the bases truncate; caylx limb 2-lobed. Hispaniola ....40. *A. chasmema*

42b. Leaves with raised reticulate venation, elliptic-ovate, the bases shallowly cordate; calyx limb 1-lobed. Mexico & British Honduras ....41. *A. ovalifolia*

41b. Pseudostipules present; leaves with raised, reticulate venation.

43a. Leaves linear to narrowly triangular, the bases acute to shallowly cordate; calyx limb 1.5-2.5 cm long. Cuba & Hispaniola ....42. *A. linearifolia*

43b. Leaves oblong to ovate, the bases cordate; calyx limb 1 cm long. Greater Antilles ....43. *A. bilabiata*

38b. Leaf bases deeply cordate, auriculate, hastate or sagittate.

44a. Calyx limb with a spatulate terminal appendage. Hispaniola.

45a. Calyx limb 2-3 cm long, including appendage; tube 4 times longer than the utricle ....44. *A. caudata*

45b. Calyx limb 6-7 cm long, including appendage; tube 2 times longer than the utricle ....45. *A. ehrenbergiana*

44b. Calyx limb not appendaged.

46a. Flowers in congested, axillary fascicles on young stems. Introduced European herbs naturalized in NE United States & adjacent Canada ....46. *A. clematitis*

46b. Flowers solitary in the axils of leaves or bracts, or fasciculate on old woody stems (cauliflorous); lianas (except *orbicularis*).

47a. Leaves variegated, white along the major veins, heart-shaped with deeply cordate-auriculate bases. Panama ....47. *A. veraguensis*

47b. Leaves not variegated.

48a. Plants stiffly hispid-pilose throughout. S Mexico, Central America & South America ....22. *A. pilosa*

48b. Plants glabrous to densely tomentulose.

49a. Leaves more than 15 cm long and 15 cm wide, deeply cordate; flowers 8 cm long, the limb about as long as the tube ....48. *A. schippii*

49b. Leaves mostly 13 cm long and 13 cm wide, or smaller.

50a. Leaves broadly triangular.
51a. Leaves membranous, the apex acute to acuminate.
52a. Calyx limb about 3 times longer than the tube; fruits cylindric-fusiform, 2.5-4.0 cm long, 1 cm wide. S Mexico to Panama ....49. *A. inflata*
52b. Calyx limb about as long as the tube; fruits short, thick-cylindric, 3 cm long, 2 cm wide. Central America, South America & the Lesser Antilles ......50. *A. anguicida*
51b. Leaves stiffly coriaceous, the apex obtuse to subemarginate.
53a. Calyx limb about as long as the tube.
54a. Calyx limb narrowed at its base, lanceolate-ovate, 1.5 cm wide, 2.5-3.0 cm long ....51. *A. carterae*
54b. Calyx limb not at all narrowed at its base, broadly triangular, 2 cm wide, 2 cm long ....52. *A. montana*
53b. Calyx limb longer than the tube.
55a. Calyx limb spatulate, 3-4 cm long, the board, terminal portion elliptic-lanceolate ....53. *A. glossa*
55b. Calyx limb steadily narrowing to the long-attenuate apex, 5 cm long ....54. *A. mycteria*
50b. Leaves oblong, elliptic or suborbiculate.
56a. Flowers about 8 cm long; plants puberulent to tomentulose.
57a. Leaves oblong; calyx glabrescent, the limb smooth. British Honduras (?) & Panama ....55. *A. chapmaniana*
57b. Leaves elliptic-oblong; calyx very densely tomentulose, the limb spotted with elevated maculae. Costa Rica ....56. *A. tonduzii*
56b. Flowers about 6 cm long or much less.

58a. Limb narrow, linear, 5 times longer than wide or more; leaves suborbiculate. Suffrutescent herbs of Mexico ....57. *A. orbicularis*

58b. Limb triangular, less than 4 times longer than wide; leaves elliptic to ovate. Woody lianas of Panama & the Lesser Antilles ....58. *A. constricta*

1. Aristolochia reticulata Nutt., Trans. Amer. Phil. Soc., n.s., **5:** 162, 1835, non Seemann (1854), nec Holton ex Duchr. (1864). (ex char.)—Fig. 3.

Siphisia reticulata (Nutt.) Klotzsch, Monatsb. Acad. Berlin **1859:** 604, 1859.

Hispid-pilose *herbs*. *Leaves* isomorphic, elliptic-sagittate, subcoriaceous, obtuse at the apex, strongly amplexicaul, subsessile, 3-7 cm broad, 7-12 cm long, the venation strongly verrucose beneath. *Pseudostipules* absent. *Flowers* in basal racemose clusters, bracteolate, geniculate, purplish-brown, the utricle subglobose, 4 mm long, syrinx indistinct, inequilaterally annular, the tube bent, 7 mm long, annulus a thin, smooth ring, the limb 3-lobed, smooth, 5 mm wide, 5 mm long. *Gynostemium* 3-lobed, 2 mm high, 3 mm broad, the anthers 6, more or less united in 3 horizontal groups. *Fruits* spheric, sub-ligneous, 12 mm diameter, dehiscence basipetal. *Seeds* few, revolute, 3 mm wide, 3 mm long, 2 mm thick.

In sandy soils of eastern Texas, southwestern Arkansas and northwestern Louisiana.

United States. arkansas: Hempstead, Little River, Miller & Pulaski counties. louisiana: Ouachita & Vernon parishes. texas: Angelina, Austin, Bowie, Harris, Harrison, Houston, Jefferson, Leon, Marion, Montgomery, Nacogdoches, Polk, San Augustine, Smith, Trinity, Upshur, Van Zandt, Walker, Waller & Young counties.

2. Aristolochia serpentaria L., Sp. Pl. 961, 1753. (Type: *Linn. Herb. London, no. 1071.7,* photo)—Fig. 4.

A. serpentaria var. *β* Willd., Sp. Pl. **4:** 159, 1805. (ex char.)
A. serpentaria var. *γ* Willd., loc. cit. 160. (ex char.)
A. sagittata Muhl., Cat. Pl. Amer. Septent. 81, 1813, nom. nud.
A. hastata Nutt., Gen. N. Amer. Pl. **2:** 200, 1818, non H.B.K. (1817), nec Jack (1822), nec Jacquin, sphalm. ex Klotzsch (1859), nec Klotzsch (1859). (ex char.)
A. polyrrhizos Sprengel, Syst. Veg., ed. 16, **3:** 754, 1826. (Based on *A. hastata* Nutt.)
A. dodecandra Raf., Med. Fl. **1:** 62, 1828, nom nud.
A. officinalis Nees, Pl. Offic. *t. 144,* 1828. (ex ic.)
Endodeca serpentaria (L.) Raf., Med. Fl. **1:** 62, 1828. (Based on *A. serpentaria* L. acc. to Bigel.)
E. hastata (Nutt.) Raf., Fl. Tellur. **4:** 99, 1836.
Pistolochia serpentaria (L.) Raf., loc. cit. 98 (ex ic. cit.)
Psophiza undulata Raf., loc. cit. 99. (Based on *A. serpentaria* L. acc. to Bigel.)
Endodeca bartonii Klotzsch, Monatsb. Acad. Berlin **1859:** 600, 1859. (Based on *A. serpentaria* L. acc. to Barton)

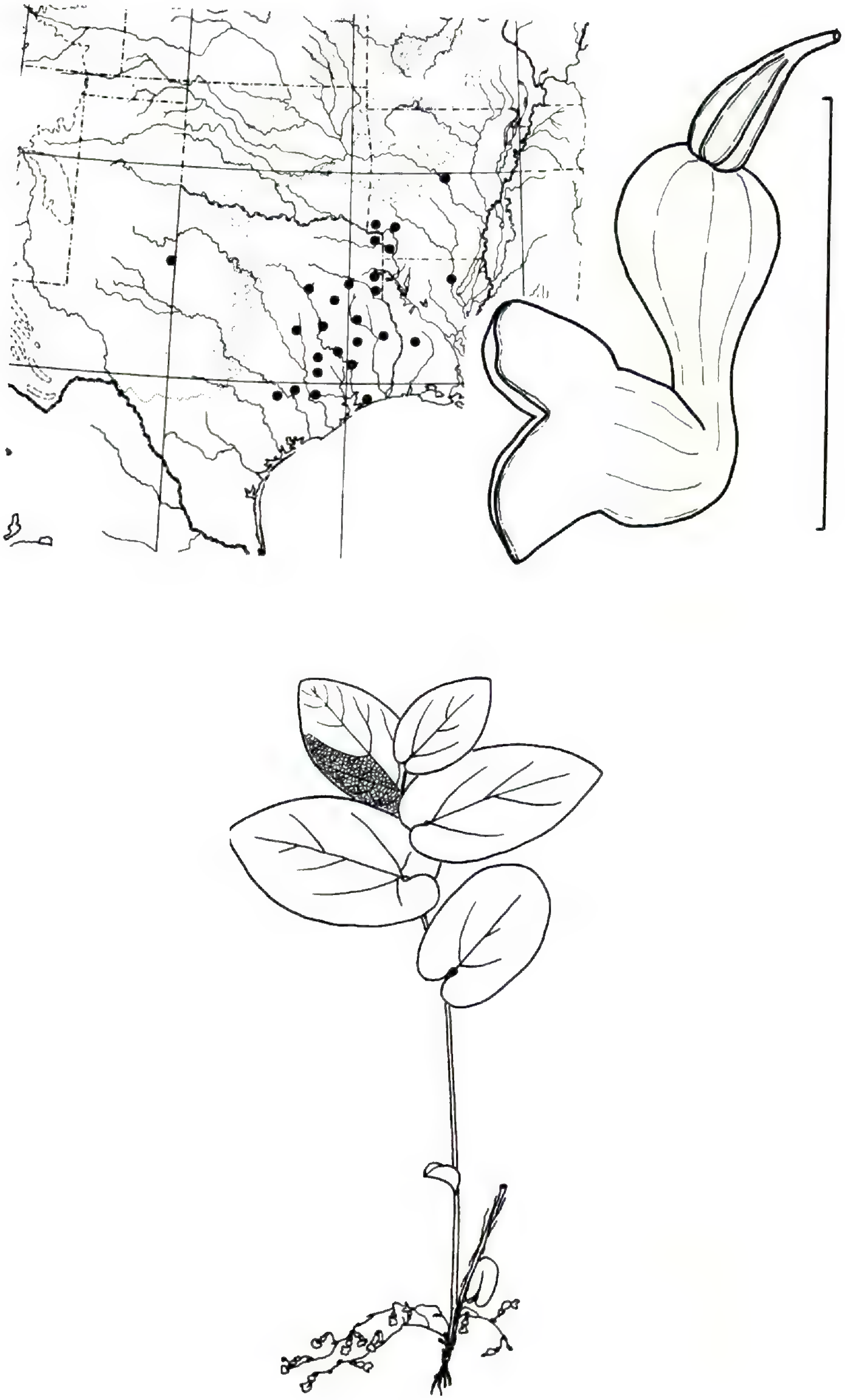


Fig. 3. Distribution, flower and habit of *A. reticulata.* (In all of the illustrations that follow, the flowers and leaves are scaled to a one centimeter line placed near the drawing; gynostemia are scaled to a one millimeter line placed near the drawing.)

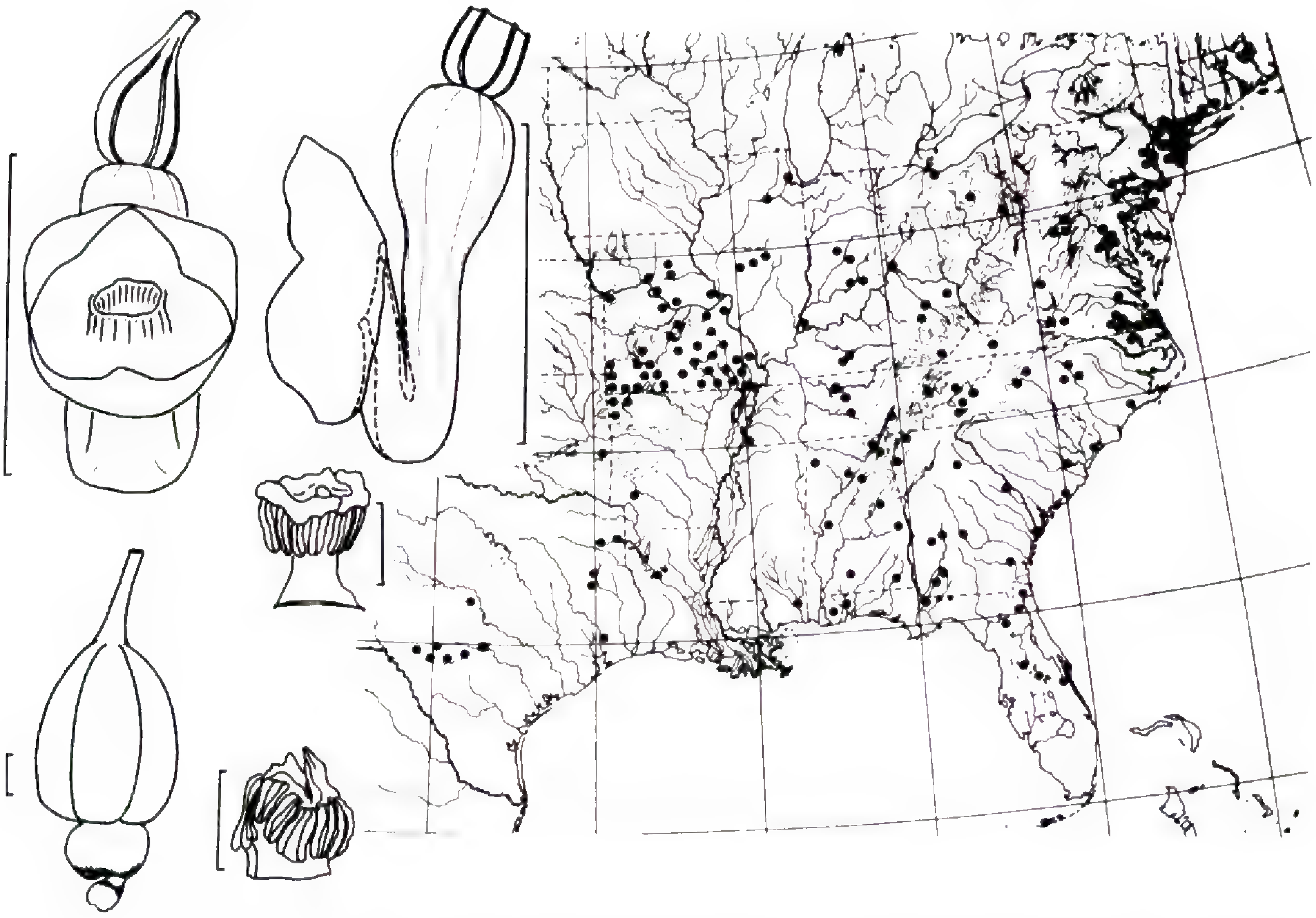


Fig. 4. Flowers, gynostemium and distribution of *A. serpentaria;* the lower left figure is a cleistogamous flower, and to its right the gynostemium of a cleistogamous flower. (The scale of the cleistogamous flower is shown by a one millimeter line.)

E. polyrrhizos (Sprengel) Klotzsch, loc. cit. 601.
Aristolochia serpentaria β bartonii (Klotzsch) Duchr. in DC., Prod. **15** (1): 433, 1864.
A. serpentaria γ laxa Duchr., loc. cit. 434. (Type: *without data,* LE; MO, photo)
A. serpentaria δ hastata (Nutt.) Duchr., loc. cit.
Endodeca dodecandra Raf. ex Jacks., Ind. Kew. **1**: 840, 1893. (= *A. dodecandra* Raf.)
Aristolochia nashii Kearney, Bull. Torrey Bot. Club **21**: 485, 1894. (Type: *Nash 1139,* GH, NY, UC, US)
A. convolvulacea Small, loc. cit. **24**: 335, 1897. (Type: *Boykin s.n.,* NY)
A. serpentaria var. *nashii* (Kearney) Ahles, Jour. Elisha Mitchell Sci. Soc. **75**: 130, 1959.

Glabrous to hispid-pilose perennial *herbs*. *Leaves* heteromorphic, narrowly lanceolate to broadly ovate, delicately membranaceous, acute to acuminate at the apex, diversely truncate, sagittate or hastate-cordate at the base, 1-5 cm broad, 5-15 cm long, smooth above, beneath, the venation subimmersed. *Pseudostipules* absent. *Flowers* borne at base of the stem in racemose clusters, bracteolate, geniculate, purplish, the utricle subglobose, 3 mm long, syrinx inequilaterally annular, the tube bent, 1 cm long, annulus a thin, smooth ring, the limb somewhat indistinctly 3-lobed, smooth, 5 mm wide, 5 mm long, subpatelliform. *Gynostemium* 3-lobed, 1.5 mm high, 1.2 mm broad, the anthers 6, more or less in 3 horizontal groups. *Fruits* spheric, subligneous, 2 cm diameter, dehiscence basipetal, valvate. *Seeds* few, revolute, 4 mm wide, 5 mm long, 2 mm thick.

Plants of rich woodland soils, throughout the south-eastern third of the United States.

United States. alabama: Baldwin, Blount, Conecuh, Cullman, Dale, DeKalb, Franklin, Hale, Jackson, Lee & Talladega counties. arkansas: Benton, Carroll, Hempstead &

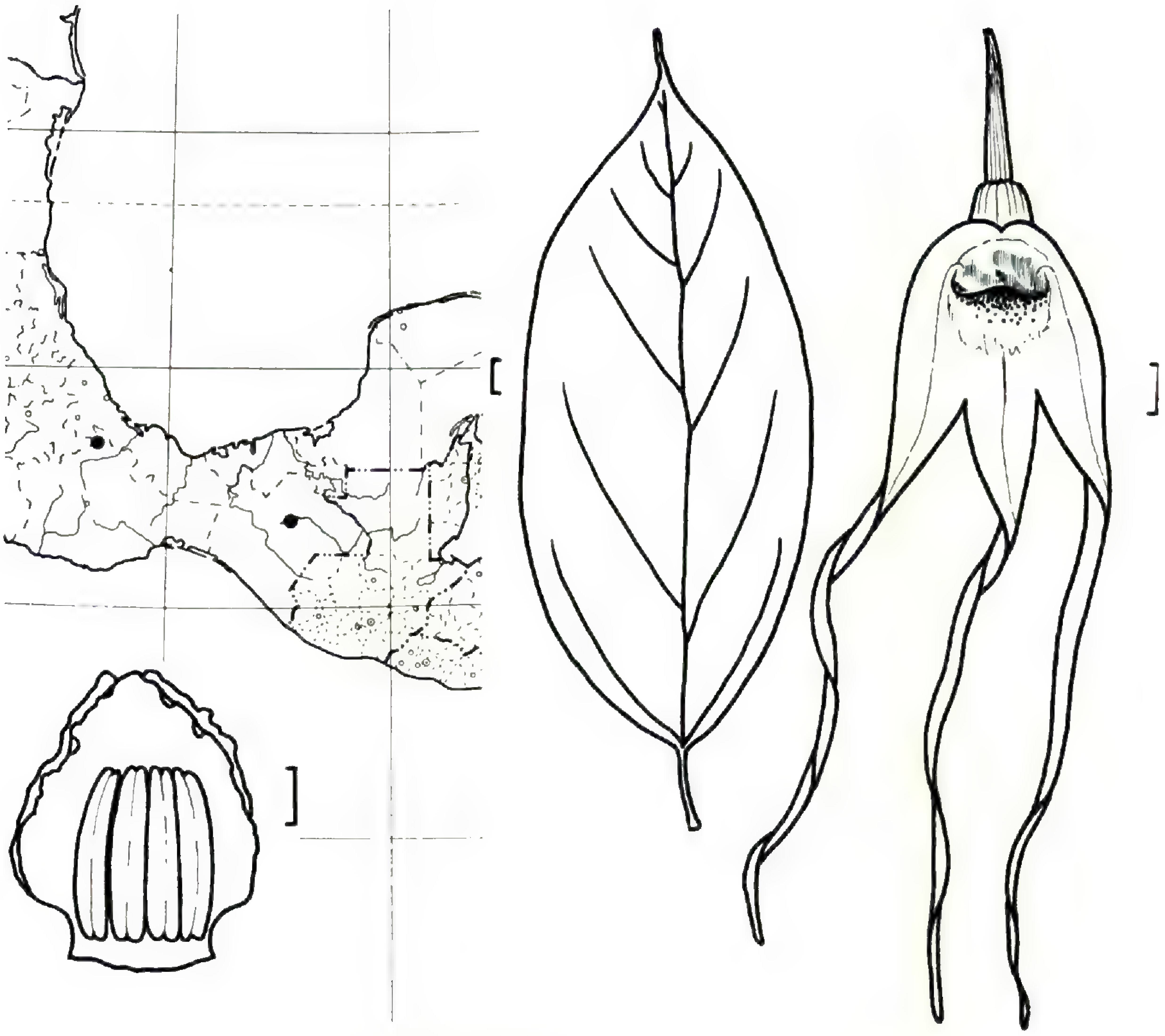


Fig. 5. Gynostemium, distribution, leaf and flower of *A. tricaudata.*

Washington counties. CONNECTICUT: Fairfield, Middlesex & New Haven counties. DELAWARE: New Castle & Sussex counties. DISTRICT OF COLUMBIA. FLORIDA: Alachua, Brevard, Clay, Columbia, Duval, Escambia, Gadsden, Lake, Monroe & Orange counties. GEORGIA: Baker, Chatham, Clarke, Dodge, Dooly, Dougherty, Floyd, Richmond, Sumter, Wayne & Whitfield counties. ILLINOIS: DePage, LaSalle, Macon, Morgan, Richland & Sangamon counties. INDIANA: Jackson, Jennings, Marion, Posey & Shelby counties. KENTUCKY: Bath, Carter, Edmonson, Estill, Harlan & Warren counties. LOUISIANA: Natchitoches parish. MARYLAND: Allegheny, Baltimore, Caroline, Montgomery & Prince Georges counties. MISSISSIPPI: George county. MISSOURI: Audrian, Barry, Benton, Bollinger, Butler, Callaway, Camden, Cape Girardeau, Carter, Cedar, Chariton, Christian, Crawford, Dallas, Dent, Douglas, Dunklin, Franklin, Gasconade, Greene, Hickory, Howard, Howell, Iron, Jackson, Jasper, Laclede, Lincoln, Linn, McDonald, Madison, Maries, Marion, Moniteau, Monroe, Montgomery, Morgan, New Madrid, Newton, Oregon, Osage, Ozark, Perry, Pettis, Pike, Pulaski, Ralls, Reynolds, Ripley, St. Francois, Ste. Genevieve, St. Louis, Scott, Shannon, Shelby, Stoddard, Stone, Taney, Texas, Vernon, Washington, Wayne & Webster counties. NEW JERSEY: Bergen, Burlington, Essex, Hunterdon, Middlesex, Monmouth, Morris, Salem & Sussex counties. NEW YORK: Bronx, Orange, Queens, Richmond, Rockland & Westchester counties. NORTH CAROLINA: Buncombe, Chatham, Forsyth, Haywood, Hertford, Iredell, Jackson, Onslow, Orange & Wake counties. OKLAHOMA: LeFlore county. OHIO: Erie, Hamilton & Holmes counties. PENNSYLVANIA: Allegheny, Berks, Bucks, Chester, Dauphin, Lancaster, Lebanon, Northampton, Philadelphia & York counties. SOUTH CAROLINA: Anderson, Charleston, Clarendon, Greenville, Horry & Williamsburg counties. TENNESSEE: Cocke, Davidson, Knox, Moore, Rutherford, Sequatchie & Shelby counties. TEXAS: Bandera, Cherokee, Edwards, Hays, Houston, Kendall, Kerr, Liberty, Marion, Real, San Saba & Upshur counties. VIRGINIA: Bath, Bedford, Brunswick, Campbell, Dinwiddie, Fairfax, Greensville, Henrico, Nansemond,

Norfolk, Princess Anne, Prince William, Shenandoah, Smyth, Southampton & Sussex counties. WEST VIRGINIA: Hampshire & Mineral counties.

The heteromorphic or polymorphic foliage of these plants is their most striking feature, and the one most likely to afford difficulty in identification.

This plant is the once-popular *serpentary* or *snake-root* of commerce. The literature catalogues its use for nearly all of the ills man falls heir to, but judging from its lack of use in modern pharmacognosy, these former uses seem to have no modern medical value.

3. Aristolochia tricaudata Lemaire, Illus. Hort. **14:** *t. 522,* 1867. (ex ic.)—Fig. 5.

Tomentulose *shrubs. Leaves* petiolate, elliptic to oblong, acuminate, basally obtuse, 6-12 cm broad, 18-22 cm long, deep green, glabrous above, beneath paler, tomentulose along the veins. *Pseudostipules* absent. *Flowers* solitary in the leaf axils (?), ebracteolate, geniculate, purple, the utricle pyriform, ca 4 cm long, syrinx absent, the tube bent, indistinguishable from the utricle except by the flexure at the apex of the utricle, ca 2 cm long, annulus absent, the limb of 3 subparallel lobes, smooth, each with a linear, pendent appendage, 4 cm wide, ca 16 cm long, overall. *Gynostemium* 3-lobed, 5 mm high, 4 mm broad, the anthers 6 in 3 horizontal groups. *Fruits* not seen.

On forested hillsides, southern Mexico.

Mexico: Chiapas, Oaxaca.

Sterile specimens of *A. tricaudata* may be confused with the foliage of *A. arborea,* but these two plants are unmistakably distinct when flowers are present. *Aristolochia tricaudata* has been, unfortunately, very rarely collected. It would make a magnificent ornamental plant.

4. Aristolochia malacophylla Standl., Proc. Biol. Soc. Wash. **33:** 65, 1920. (Type: *Pringle 13424,* GH, MEXU, US)—Fig. 6.

A. sericea Benth., Pl. Hartweg. 81, 1841, non Blanco (1837) (Type: *Hartweg* 565 P; photos F, MO, NY, US)
A. mexiae Standl., Field Mus. Pub. Bot. **8:** 136, 1930. (Type: *Mexia 2772,* A, F, MO, NY, UC)

Sprawling tomentose *shrubs. Leaves* variable, petiolate, elliptic to oblong, obtuse at the apex, basally sagittate to cordate, 4-7 cm broad, 8-12 cm long, tomentulose along the veins above, beneath woolly tomentose. *Pseudostipules* absent. *Flowers* on short, axillary leafless, bracteolate branches, geniculate, purple and yellow, the utricle long-ovoid, 3 cm long, syrinx absent, the tube indistinguishable from the utricle except by the flexure at its origin at the apex of the utricle, 3 cm long, annulus absent, the limb smooth, 3-lobed, the lobes parallel, directed downward, each with a linear, pendent, tapelike appendage, 1 cm wide, ca 4 cm long overall. *Gynostemium* 3-lobed, 3 mm high, 3 mm broad, the anthers 6 in 3 horizontal groups. *Fruits* woody, 5 cm long, 2 cm wide, dehiscence basipetal, valvate (?). *Seeds* numerous, revolute.

Fig. 6. Distribution, leaf, gynostemium and flower of *A. malacophylla*.

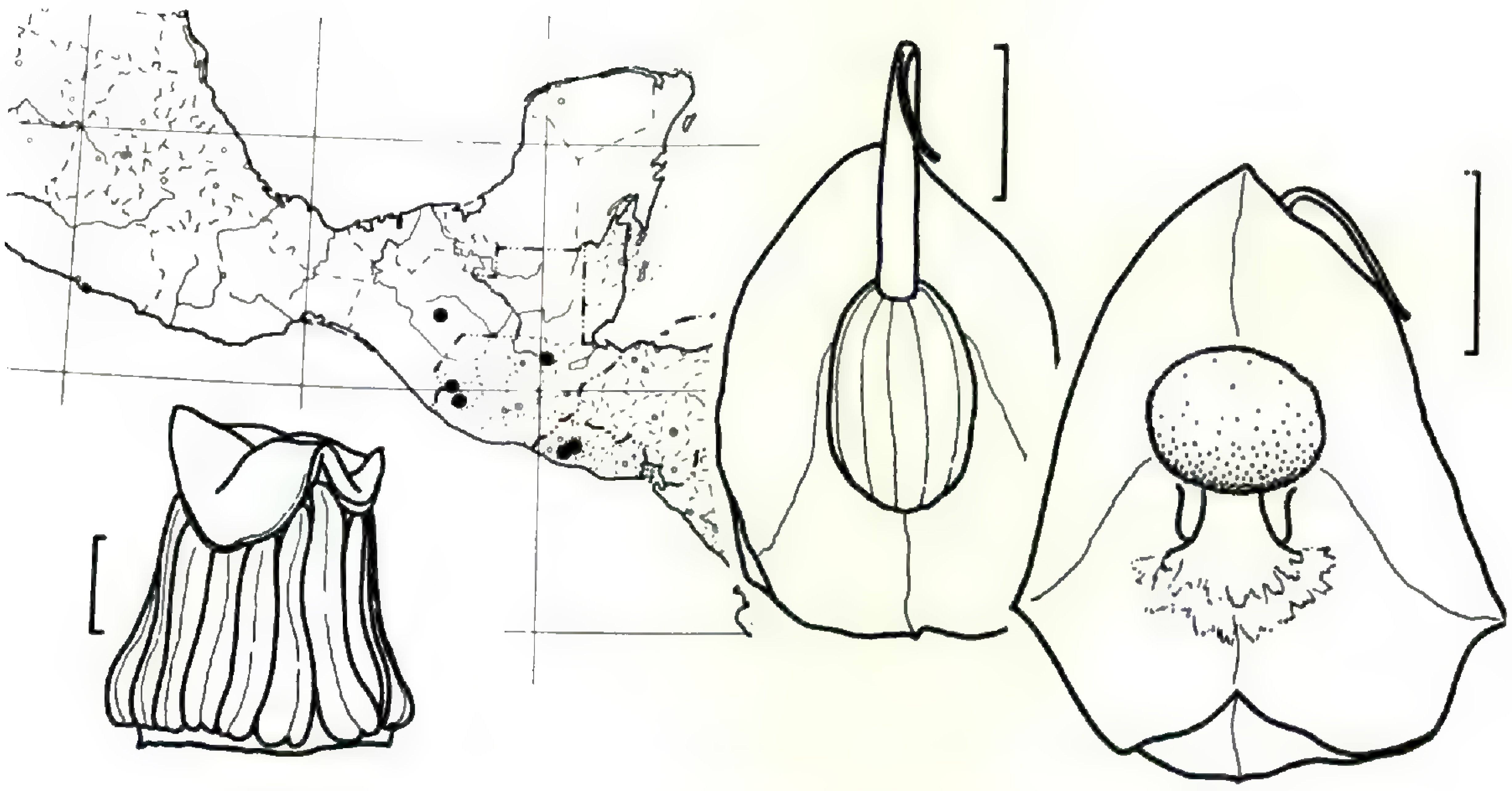


Fig. 7. Distribution, gynostemium and flowers of *A. arborea*.

In open pine-oak forests, in dry or wet situations, west Mexico eastward to Honduras.

Mexico: Chiapas, Jalisco, Michoacán.
Guatemala: Sacatepequez.
Honduras: Comayagua, Morazán.

As in most other species, *A. malacophylla* requires flowering material for accurate identification. It has been the custom to call any tomentose, oblong-leaved species *A. sericea;* however, this familiar name must yield to the earliest synonym *A. malacophylla* Standl.

5. Aristolochia arborea J. Linden, Cat. Pl. **13:** 6, 1858. (ex char.)—Fig. 7.

A. salvadorensis Standl., Jour. Wash. Acad. Sci. **13:** 367, 1923. (Type: *Calderón 1484,* US)
A. steyermarkii Standl., Field Mus. Pub. Bot. **22:** 329, 1940. (Type: *Steyermark 33455,* F)

Finely tomentulose *shrubs* or small *trees. Leaves* petiolate, rather variable, narrowly elliptic, ovate, obovate or oblong, acuminate, basally subtruncate to acute, 4-10 cm broad, 9-25 cm long, green and smooth above, beneath rusty-tomentulose, particularly along the veins. *Pseudostipules* absent. *Flowers* in cauliflorous, many branched, bracteolate, racemose clusters, geniculate, purple, the utricle ellipsoid, 2 cm long, syrinx absent, the tube bent, 1 cm long, annulus absent, the limb smooth, 3-lobed, the lobes acute, divergent, 2.5-3.0 cm wide, 3-4 cm long, the limb with a large, inflated, capitate, stipitate, bulla or boss below the tube orifice. *Gynostemium* barely 3-lobed, the anthers 6, equidistant. *Fruits* woody, ca 3 cm long, ca 1.5 cm wide or larger, dehiscence basipetal, subvalvate (?). Mature *seeds* not seen.

On moist mountainsides, Mexico to El Salvador.

Mexico: Chiapas.
Guatemala: Alta Verapaz, Quetzaltenango, San Marcos.
El Salvador: La Libertad, San Salvador.

Calderón reports the vernacular name, *guaquito de la tierra,* in El Salvador; Steyermark, *guaco de montaña,* in Guatemala. Broadway, who collected it from cultivated plants in Trinidad, mentions that the flowers resemble bats clinging to the plant on the old wood.

6. Aristolochia **bullata** Pfeifer, sp. nov.—Fig. 8.

Caules subprostrati flexuosi volubiles. *Folia* ignota. *Flores* multi paniculati parum bracteolati geniculati purpurei; utriculus ovoideus 1.5 cm longus; syrinx absens; tuba absens; foramen utriculi a latere; limbus 3-lobus patulus 4 cm latus 3.5 cm longus cum bulla una magna tumida sessili infra foramen tubam. *Columna* 3-loba 3 mm alta 2.5 mm lata; stamina 6 ad libram in catervis 3. *Fructus* ignotus.—Holotypus: *Hinton 14569,* US ("forested hillside; procumbent vine in shade; local: Atoyac; alt. 25-100 m.; Distr. Galeana, Guerrero, Mexico."). Isotypi GH, NY.

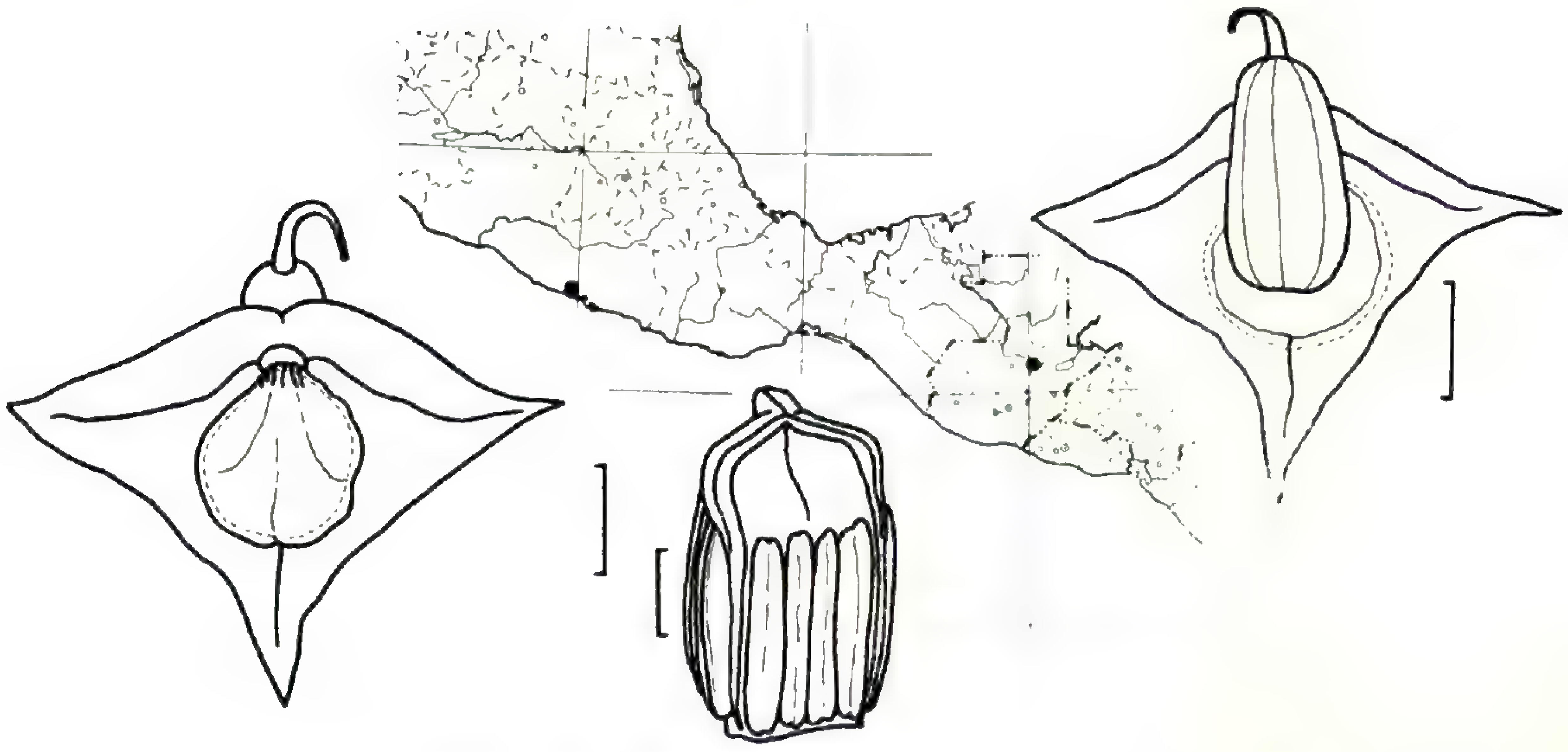


Fig. 8. Flowers, gynostemium and distribution of *A. bullata.*

Large procumbent *lianas.* Vegetative parts not seen. *Flowers* in several-flowered, long, several-branched, bracteolate, cauliflorous, racemose clusters, geniculate, purple, the utricle ovoid, 1.5 cm long, syrinx merely a stricture at the side of the utricle, opening onto the limb, the tube absent, the limb of 3 divergent lobes, with a large, inflated, umbonate, sessile bulla or boss below the tube orifice, 4 cm wide, 3.5 cm long. *Gynostemium* 3-lobed, 3 mm high, 2.5 mm broad, the anthers 6, in 3 groups. *Fruits* not seen.

I have seen one other specimen, *von Tuerckheim (JDS) 8452,* US. ("Cubilquitz, Depart. Alta Verapaz, Guatemala, alt. 350 m., M. Jul. 1903.")

Aristolochia bullata is especially distinctive; the inflated bulge or "blister" on the limb sets it apart from all other species. It should be sought by collectors in the areas between the two distant localities cited here.

7. Aristolochia **paracleta** Pfeifer, nom. nov.—Fig. 9.

A. mollis Standl. & Steyerm., Field Mus. Pub. Bot. **23:** 155, 1944, non Dunn (1908). (Type: *Steyermark 51269,* F, NY, US)

Wooly *lianas. Leaves* petiolate, elliptic to suborbiculate, obtuse at the apex, basally cuneate-obtuse, 6-15 cm broad, 10-20 cm long, smooth above, beneath tomentulose. *Pseudostipules* absent. *Inflorescence* few-flowered, racemose. *Flowers* geniculate, the utricle gradually contracted to an eccentric tubular base, 3 cm long, the syrinx extending in a ridge downward onto the limb, the tube not delimited by a constriction from the utricle and limb, the limb unequally 3-lobed, 2.0-3.5 cm long, the median lobe lowest, unappendaged. *Gynostemium* 3-lobed, narrowly columnar, 1 cm tall, 0.4 cm broad, the anthers 6, in 3 horizontal groups. *Fruits* not seen.

Known only from the type locality.

Guatemala: Huehuetenango.

This species is reported by Dr. Julian Steyermark to be used in treating gas on the stomach; the leaves are boiled to make a tea. It is called *hoja aire* in Guatemala.

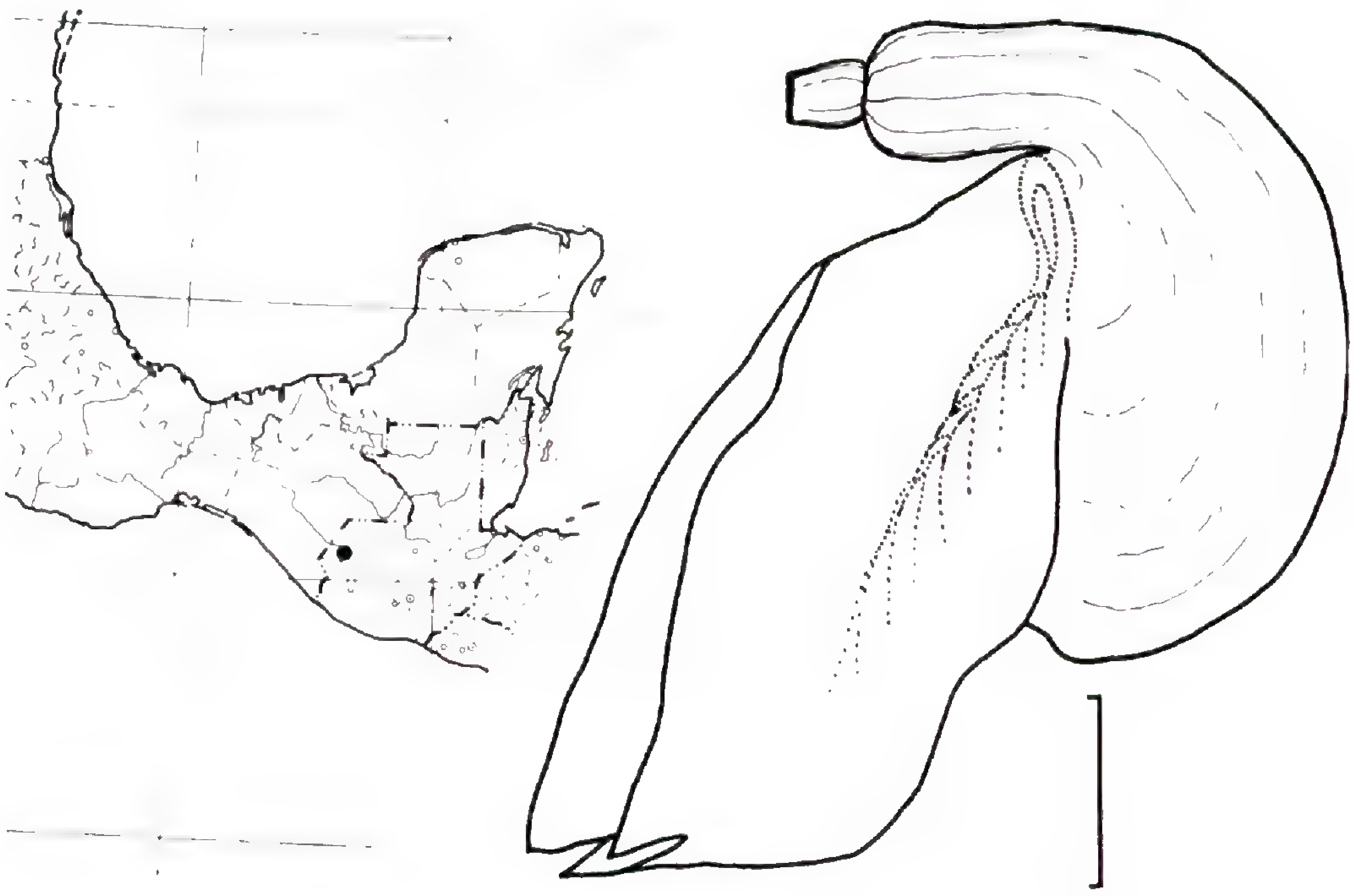


Fig. 9. Distribution and flower of *A. paracleta.*

Accurate identification of this plant requires dissection of flowers. It may be confused, on the basis of superficial vegetative and floral appearances, with *A. rhizantha, A. thwaitesii* and *A. arborea* as well as other Central American species with tomentose leaves.

8. Aristolochia panamensis Standl., Jour. Wash. Acad. Sci. **15:** 5, 1925. (Type: *Standley 29906,* A, US)—Fig. 10.

Low, pubescent *shrubs. Leaves* petiolate, elliptic-ovate, acute to acuminate, basally acute to attenuate, 5-12 cm broad, 10-23 cm long, green and smooth above, beneath paler, silvery-pubescent. *Pseudostipules* absent. *Flowers* in several-branched, bracteolate, cauliflorous, racemose clusters near the soil level, geniculate, purple, the utricle subpyriform but gradually contracted to an eccentric, tubular base, syrinx inequilaterally annular, 3 cm long, the tube absent, the limb smooth, 3-lobed, sub-inflated, 1.5 cm wide, ca 2 cm long, unappendaged. *Gynostemium* 3-lobed, 5 mm high, 4 mm broad, the anthers 6 in 3 horizontal groups. *Fruits* ellipsoid-cylindric, woody, 2.5 cm long, 1.5 cm wide, dehiscence basipetal, valvate, the hypanthium absent. *Seeds* few, strongly revolute, pyramidal, 4 mm wide, 5 mm long, 4 mm thick.

In open savannahs; known only from Panama.

Panama: Chiriquí, Canal Zone.

In habit, *A. panamensis* is least like any preconception of an *Aristolochia* one might have; if it is once identified to genus, there is little else in *Aristolochia* it vegetatively resembles. The flowers show its close alliances to the other species of Central America with 3-lobed calyx limbs.

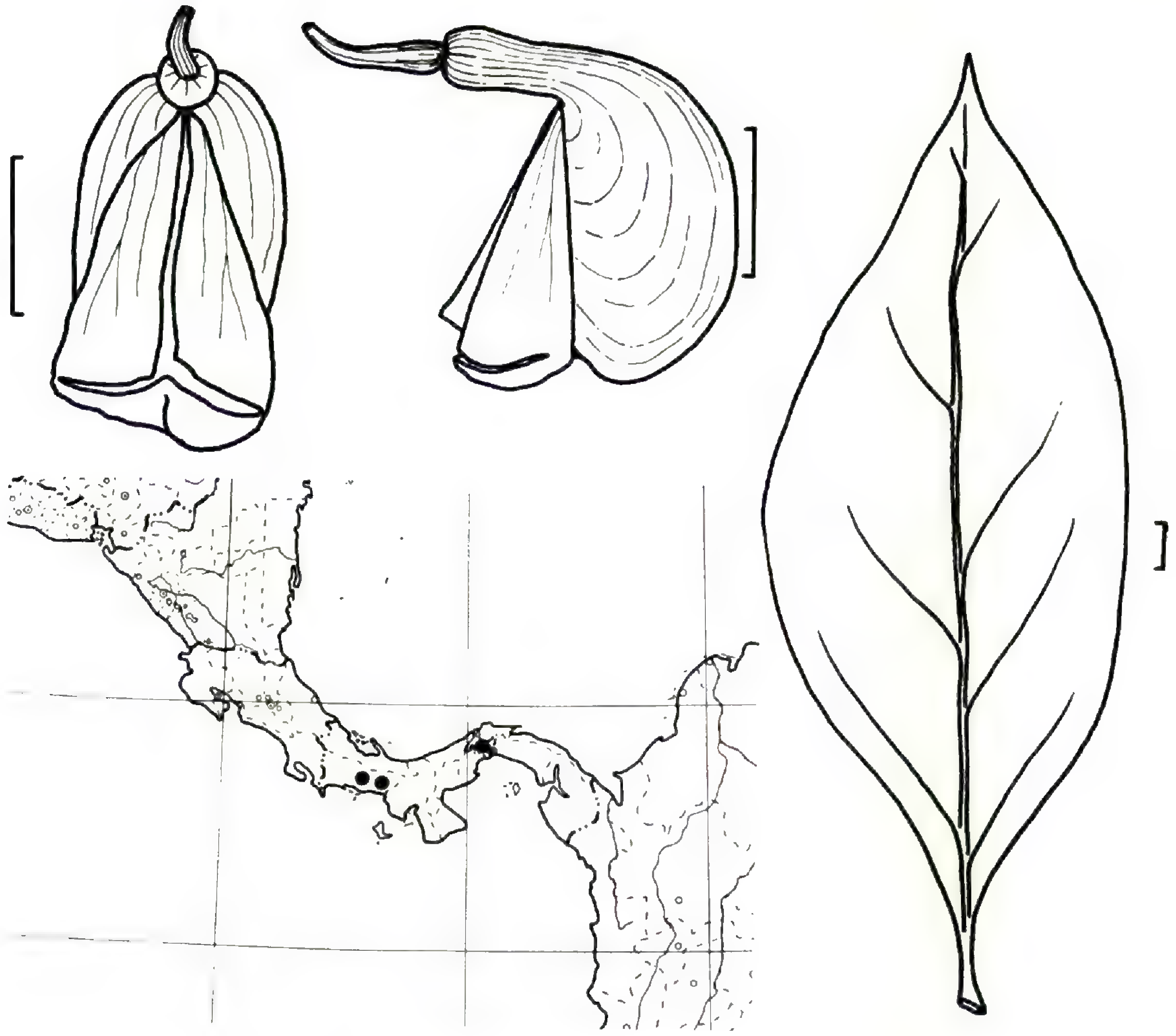


Fig. 10. Flowers, distribution and leaf of *A. panamensis.*

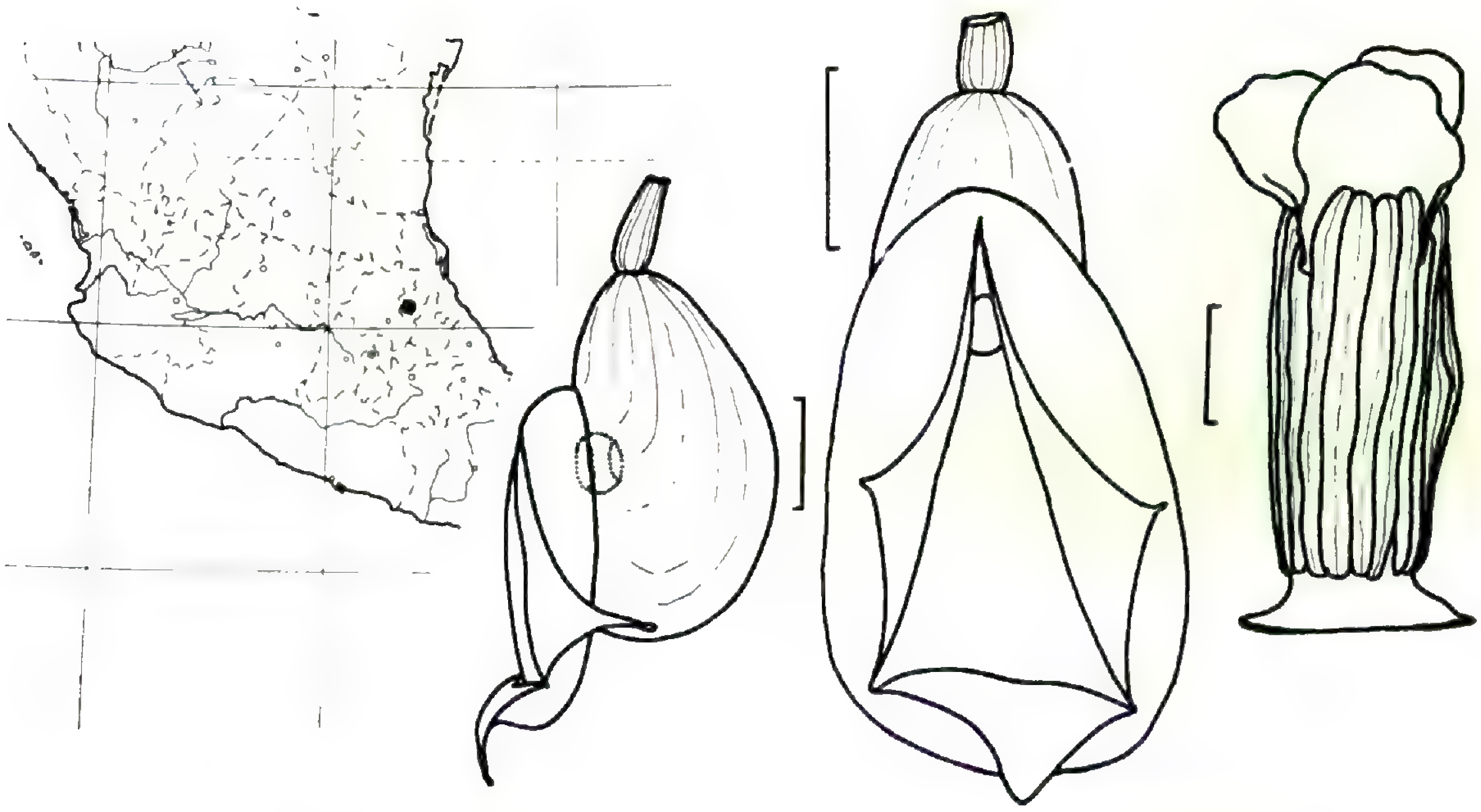


Fig. 11. Distribution, flowers and gynostemium of *A. asclepiadifolia.*

9. Aristolochia asclepiadifolia Brandg., Univ. Calif. Pub. Bot. **6:** 178, 1915. (Type: *Purpus 7394,* F, GH, MO, NY, UC, US)—Fig. 11.

Tomentulose sprawling *shrubs* or *lianas*. *Leaves* sub-sessile, auriculate, amplexicaul, elliptic-obovate, obtuse at the apex, 5-10 cm broad, 8-17 cm long, rough-strigose above, beneath tomentulose. *Pseudostipules* absent. *Flowers* in few-flowered, short axillary racemes, bracteolate, geniculate, purple, the utricle abruptly contracted at the base, ovoid, 3 cm long, syrinx urceolate, the tube absent, the limb smooth, 3-lobed, 2 cm wide, the median lobe lowest. *Gynostemium* narrowly columnar, 3-lobed, 5 mm high, 2 mm broad, the anthers 6 in 3 horizontal groups. *Fruits* very woody, 3.5-6.0 cm long, 2-3 cm wide, dehiscence acropetal, septifragal, the hypanthium absent. *Seeds* numerous, revolute, 5 mm wide, 5 mm long, 3 mm thick.

Growing on rocks at low elevations along the eastern coast of Vera Cruz.

Mexico: Vera Cruz.

This species is easily distinguished from its close relatives by the urceolate syrinx and clasping leaves. If one is acquainted with those species of *Asclepias* with heavy, large felty leaves, the name *asclepiadifolia* is a useful mnemonic device.

10. Aristolochia rhizantha Lundell, Field & Lab. **6:** 10, 1937. (Type: *Lundell & Lundell* 7257, MICH, NY, S, US)—Fig. 12.

Tomentulose clambering *shrubs*. *Leaves* petiolate, broadly elliptic, obtuse at the apex, truncate to shallowly cordate at the base, 12-15 cm broad, 20-25 long, strigose, deep green above, beneath tomentulose, paler. *Pseudostipules* absent. *Flowers* on many-branched compound-racemose basal inflorescences, bracteolate, geniculate, the utricle abruptly contracted at the base, 1 cm long, the syrinx tubular, sharply oblique, the tube absent, the limb rugose-warty, 3-lobed, the median lobe lowest, 2 cm long. *Gynostemium* narrowly columnar, 3-lobed, 7 mm high, 3 mm broad, the anthers 6 in 3 horizontal groups. *Fruits* ligneous, narrowly cylindric, 4 cm long, 1.2 cm wide, dehiscence acropetal, valvate, the hypanthium absent. *Seeds* few, revolute, 3 mm wide, 4 mm long, 3 mm thick.

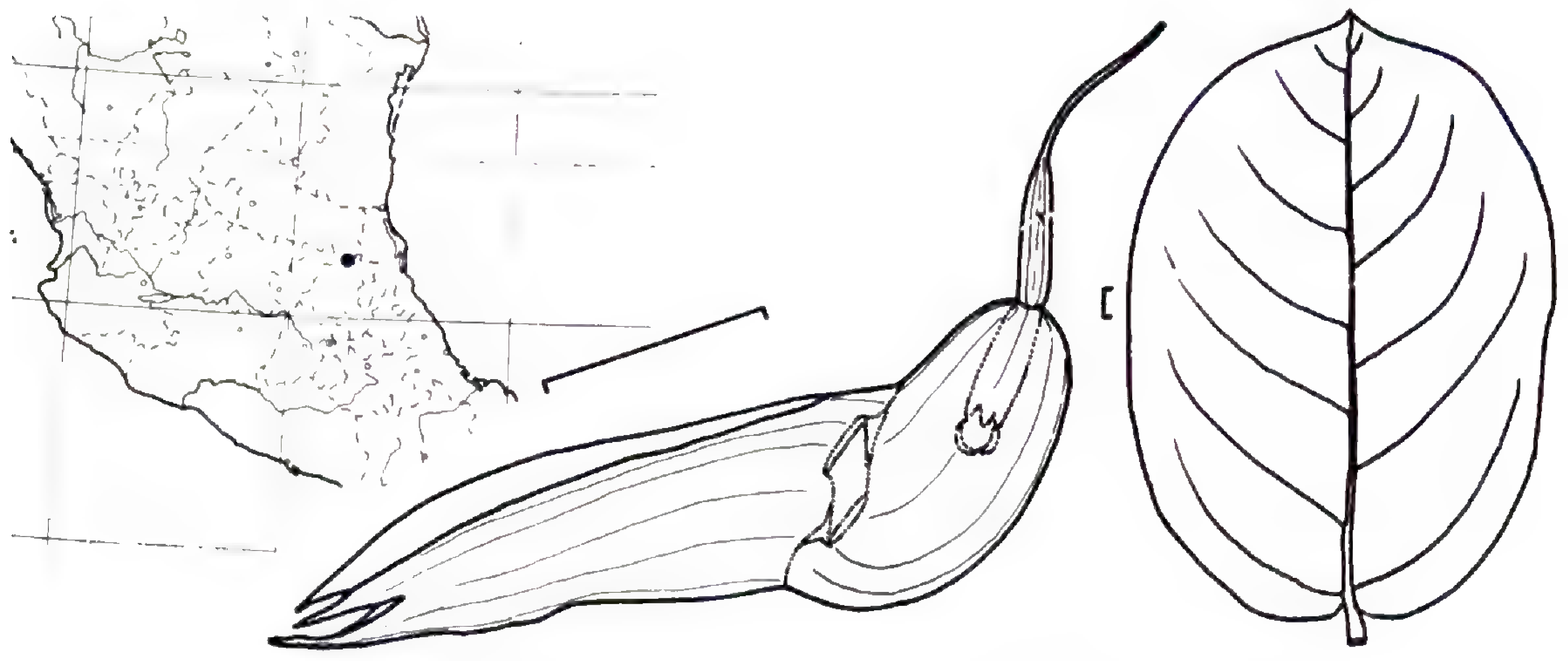


Fig. 12. Distribution, flower and leaf of *A. rhizantha*.

Found in low forests on mountain side, Sierra Madre Oriental, near Tamazunchale. Known only from the type collection.

MEXICO: San Luis Potosí.

A very distinctive species, *A. rhizantha* is unique in its sharp reduction of the syrinx and tube into the oblique, tubular syrinx which affords passage into the utricle. During the winter of 1961-2, much of the vegetation of northeastern Mexico was badly frozen, including the area around Tamazunchale, in an unprecedented (in recorded times) cold wave; it is not unreasonable to expect that the colony of *A. rhizantha* was killed, along with many of the tree ferns and other exotics which made the area so interesting from a botanical viewpoint. (A recent visit showed the flora nearly recovered, but it has not been possible to locate plants of *A. rhizantha.*)

11. ARISTOLOCHIA THWAITESII Hook., Bot. Mag. *t. 4918,* 1856. (ex ic.)—Fig. 13.

Small, woody *shrubs* or *lianas. Leaves* elliptic-ovate, obtuse at the apex, the base sagittate-auriculate to cuneate, 4-8 cm broad, 10-20 cm long, smooth above, beneath woolly. *Pseudostipules* absent. *Inflorescences* racemose, bracteolate, at base of stem. *Flowers* geniculate, the utricle more or less swollen, 1.5 cm long, the syrinx absent, the tube not constricted, scarcely differentiated from the utricle and limb, the limb unequally 3-lobed, 1 cm wide, 2 cm long, the median lobe lowest, unappendaged. *Gynostemium* 3-lobed, narrowly columnar, 1 cm high, 0.4 cm broad, the anthers 6 in 3 horizontal groups. *Fruits* not seen.

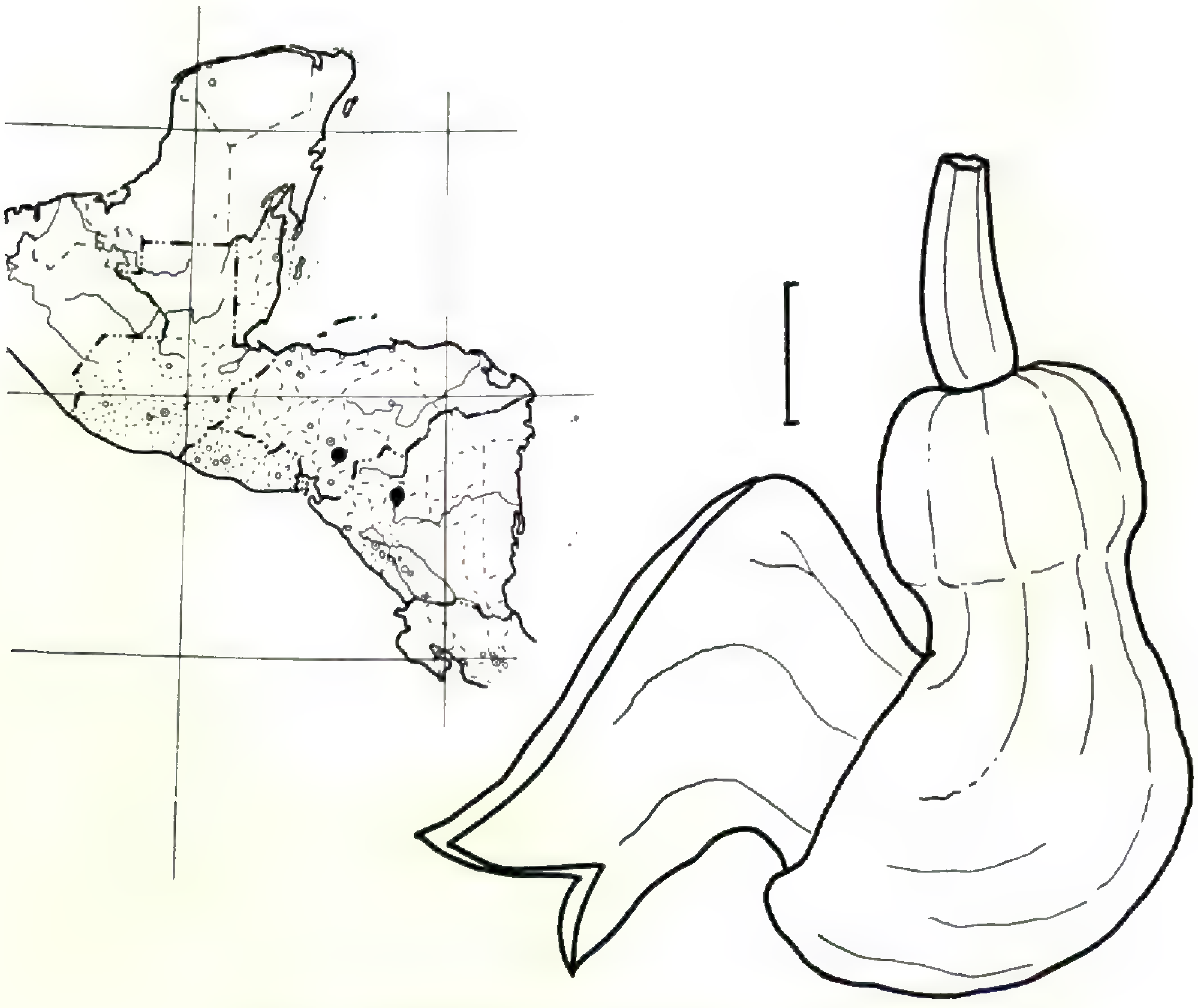


Fig. 13. Distribution and flower of *A. thwaitesii.*

Dense, wet, rocky forests in Honduras and Nicaragua.

HONDURAS: Morazán.
NICARAGUA: Jinotega.

Originally describing *A. thwaitesii* as being from Ceylon, Hooker later (Bot. Mag. *t.* 5295) mentioned the improbability of this information; the illustration supplied with his description is superlative, showing an obvious relationship to the curious Central American *A. arborea*. A search for material from Central America matching the illustration yielded specimens agreeing with his description, and prompted me to reassign the name. There is little doubt that these are the plants described by Hooker.

12. ARISTOLOCHIA MACROPHYLLA Lam., Encycl. Méth. Bot. **1:** 255, 1783, non Duchr. (1854). (ex char.)—Fig. 14.

A. sipho L'Herit., Stirp. Nov. 13. *t.* 7, 1784. (ex ic.)
A. frutescens Marsh, Arb. Am. 24, 1785. (ex char.)
A. grandifolia Salisb., Prod. 215, 1796. (ex char.)
Isotrema sipho (L'Herit.) Raf., Amer. Monthly Mag. & Crit. Rev. **4:** 195, 1819.
Hocquartia macrophylla (Lam.) Dum., Comm. Bot. 30, 1822.
Aristolochia arkansaw Lodd., Cat. Pl., ed. 14, 37, 1826, nom. nud. (*A. arkansana* auct.)
Siphisia glabra Raf., Medic. Fl. **1:** 65, 1828. (Based on *A. sipho* L'Herit.)
S. sipho (L'Herit.) Raf., loc. cit. 62.
Isiphia glabra (Raf.) Raf., loc. cit. **2:** 232, 1830.
Isotrema durius (Hill) H. Huber, Mitt. Bot. Staatssam. München **3:** 550, 1960. (Based on *A. macrophylla* Lam.)

Glabrescent *lianas*. *Leaves* broadly cordate, acute to obtuse at the apex, basally cordate, 7-45 cm broad, 7-50 cm long, glabrous above, beneath finely puberulent

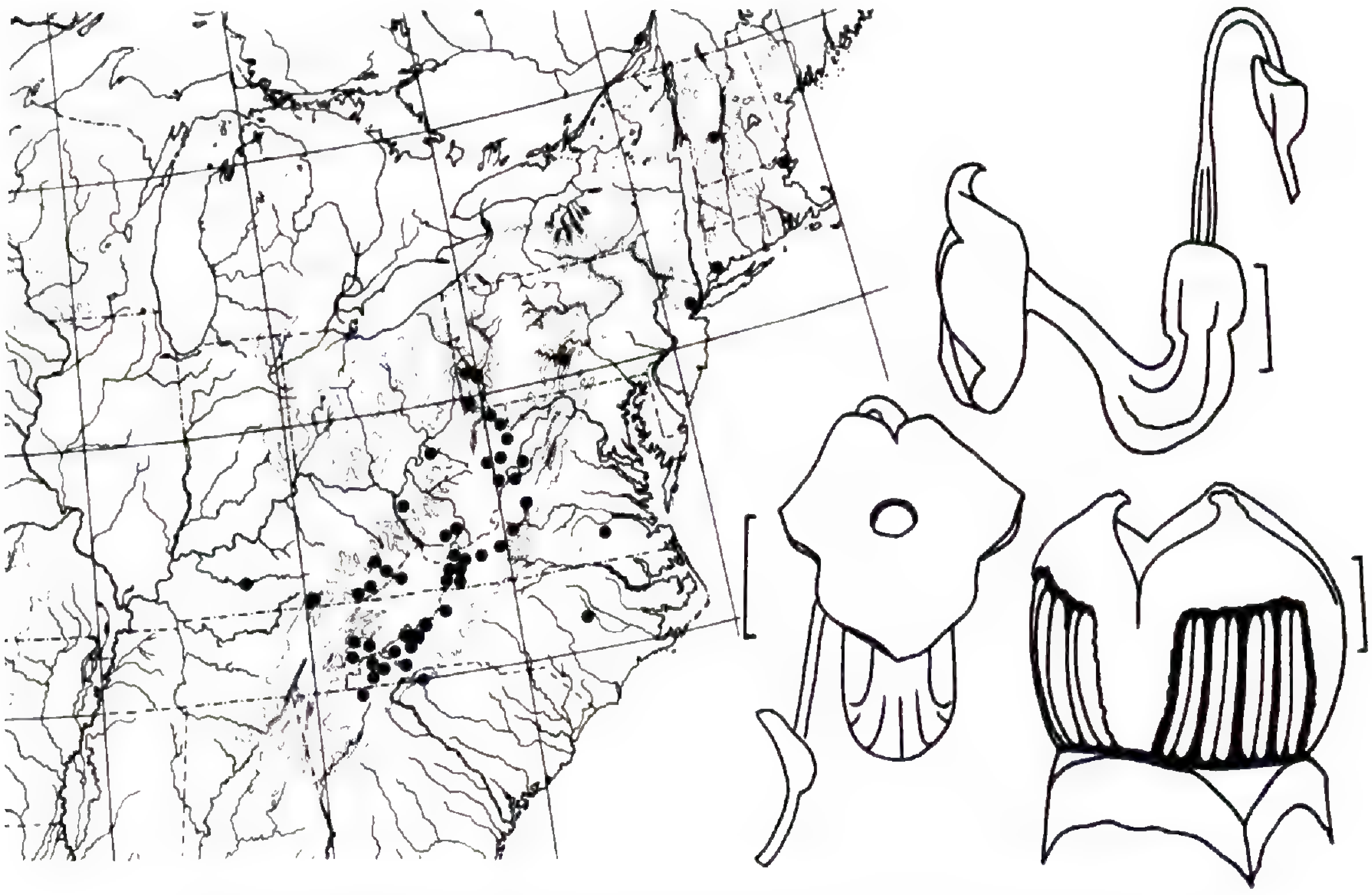


Fig. 14. Distribution, flowers and gynostemium of *A. macrophylla*.

to glabrous. *Pseudostipules* absent. *Flowers* solitary in the leaf axils, bracteolate, geniculate, green spotted with purple, brown and yellow, the utricle cylindric, 0.5 cm long, syrinx absent, the tube curved upward at its center, narrowing to the limb, 2.5 cm long, the annulus diminutive, a slightly raised, smooth ring or absent, the limb smooth, 3-lobed, 2 cm wide, 2 cm long, the lobes concave, divergent, subequal, unappendaged. *Gynostemium* squat, 3-lobed, 4 mm high, 6 mm broad, the anthers 6 in 3 horizontal groups. *Fruits* woody, persistent, glabrous to puberulent, 6-8 cm long, 4-6 cm wide, dehiscence valvate, hypanthium absent. *Seeds* numerous, flat, 1 cm wide, 1 cm long, 1 mm thick.

In rich forest soils in the Appalachian mountains.

UNITED STATES. CONNECTICUT: Fairfield county. GEORGIA: Towns county. KENTUCKY: Bell, Edmonson, Harlan, Letcher, Perry & Wayne counties. MASSACHUSETTS: Essex county. NEW JERSEY: Hudson county. NORTH CAROLINA: Buncombe, Hayward, Jackson, Johnston, Macon, Madison, Mitchell, Swain, Transylvania, Watauga & Yancey counties. PENNSYLVANIA: Allegheny, Beaver, Greene & Huntingdon counties. SOUTH CAROLINA: Greenville county. TENNESSEE: Blount, Knox, Morgan & Sevier counties. VERMONT: Windsor county. VIRGINIA: Bedford, Botetourt, Dinwiddie, Giles, Grayson, Highland, Montgomery, Roanoke, Rockbridge, Smyth, Washington, Wise & Wythe counties. WEST VIRGINIA: Monogalia, Pendleton, Pocahontas, Preston, Raleigh, Randolph, Summers, Tucker, Upshur, Wayne, Webster & Wirt counties.

This species is known throughout the eastern United States as *A. durior* Hill, based on an illustration of Hill's which more closely resembles *Bignonia capreolata* L. than *Aristolochia.* (See Pfeifer, Status of the name *Aristolochia durior* Hill. Baileya **10:** 4-7, 1962).

13. ARISTOLOCHIA CALIFORNICA Torr., Pacif. Rail. Rep. **4:** 128, 1857. (Type: *Bigelow s.n.*, NY)—Fig. 15.

Isotrema californicum (Torr.) H. Huber, Mitt. Bot. Staatssam. München **3:** 550, 1960.

Woolly to tomentose *lianas*. *Leaves* broadly cordate, acute to obtuse at the apex, basally cordate, rarely pandurate, 3-10 cm broad, 4-12 cm long, strigose above, tomentose beneath. *Pseudostipules* absent. *Flowers* solitary in the leaf axils, bracteolate, geniculate, purplish, the utricle bladdery, U-shaped, unevenly inflated, ca 3 cm long, not at all differentiated into utricle and tube, syrinx absent, abruptly narrowed at the limb, a distinct annulus absent, the limb 3-lobed, smooth, 2 cm wide, 2 cm long, the lobes concave, divergent. *Gynostemium* cylindric, deeply 3-lobed, 5 mm high, 5 mm broad, the anthers 6 in 3 horizontal groups. *Fruits* cylindric, ribbed, puberulent, 6 cm long, 2.5 cm wide, dehiscence valvate, hypanthium absent. *Seeds* numerous, flat, 1 cm wide, 1 cm long, 1 mm thick.

Generally along stream sides in California, north and east of San Francisco.

UNITED STATES. CALIFORNIA: Butte, Colusa, Contra Costa, Marin, Napa, Placer, Sacramento, San Francisco, Shasta, Siskiyou, Solano, Sonoma, Sutter, Tehama, Yolo & Yuba counties.

Very closely related to *A. macrophylla* and *A. tomentosa* of the eastern United States, *A. californica* is nevertheless very distinct. The lack of structural definition

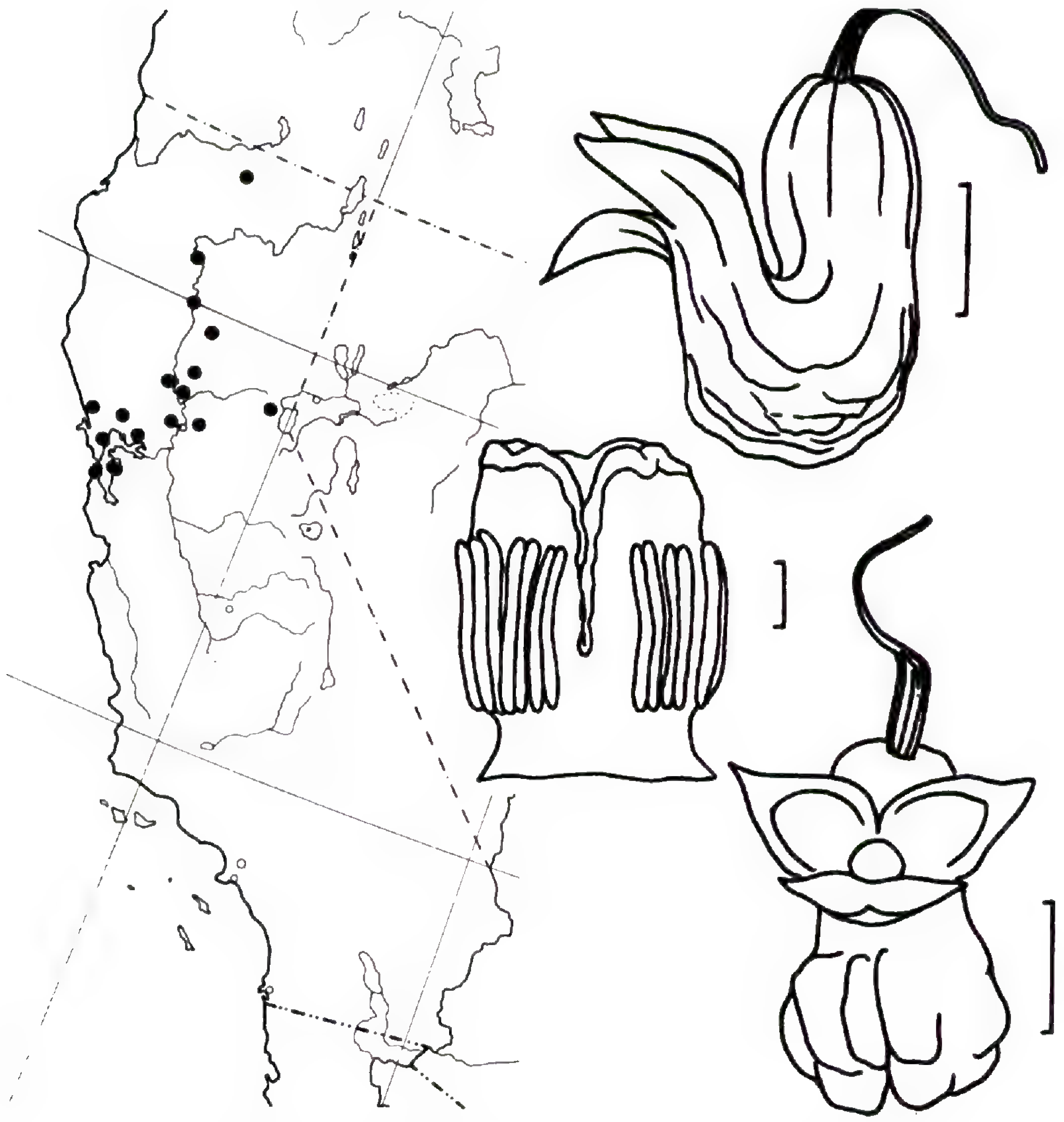


Fig. 15. Distribution, gynostemium and flowers of *A. californica.*

between utricle and tube in the flower, occurring through excessive inflation of the tube, sets it apart from the other two species.

Aristolochia californica is widely cultivated in California by persons interested in natural curiosities. This fact may be an explanation for unverified reports of *A. californica* far to the south of the range reported here.

14. Aristolochia tomentosa Sims, Bot. Mag. *t. 1369,* 1811. (ex ic.)—Fig. 16.

A. hirsuta Muhl., Cat. Pl. Amer. Septent. 81, 1813, non L. (1767), nom. nud.
A. tripteris Raf., Fl. Ludov. 24, 1817. (ex char.)
Hocquartia tomentosa (Sims) Dum., Comm. Bot. 30, 1822.
Dasyphonion tomentosum Raf., First Cat. Bot Gard. Transylv. Univ. 13, 1824. (Based on *A. tomentosa* Sims acc. to Merrill, 1949)
Siphisia tomentosa (Sims) Raf., Medic. Fl. **1:** 65, 1828.
Isiphia tomentosa (Sims) Raf., loc. cit. **2:** 232, 1830.
Aristolochia coriacea Raf., Atl. Jour. **1:** 146, 1832. (=*A. tomentosa* Sims acc. to Merrill, 1949)
A. hitchcockii Gandoger, Bull. Soc. Bot. France **66:** 232, 1919. (Type: *Hitchcock 809,* GH, MO, NY, US)
Isotrema tomentosum (Sims) H. Huber, Mitt. Bot. Staatssam. München **3:** 550, 1960.

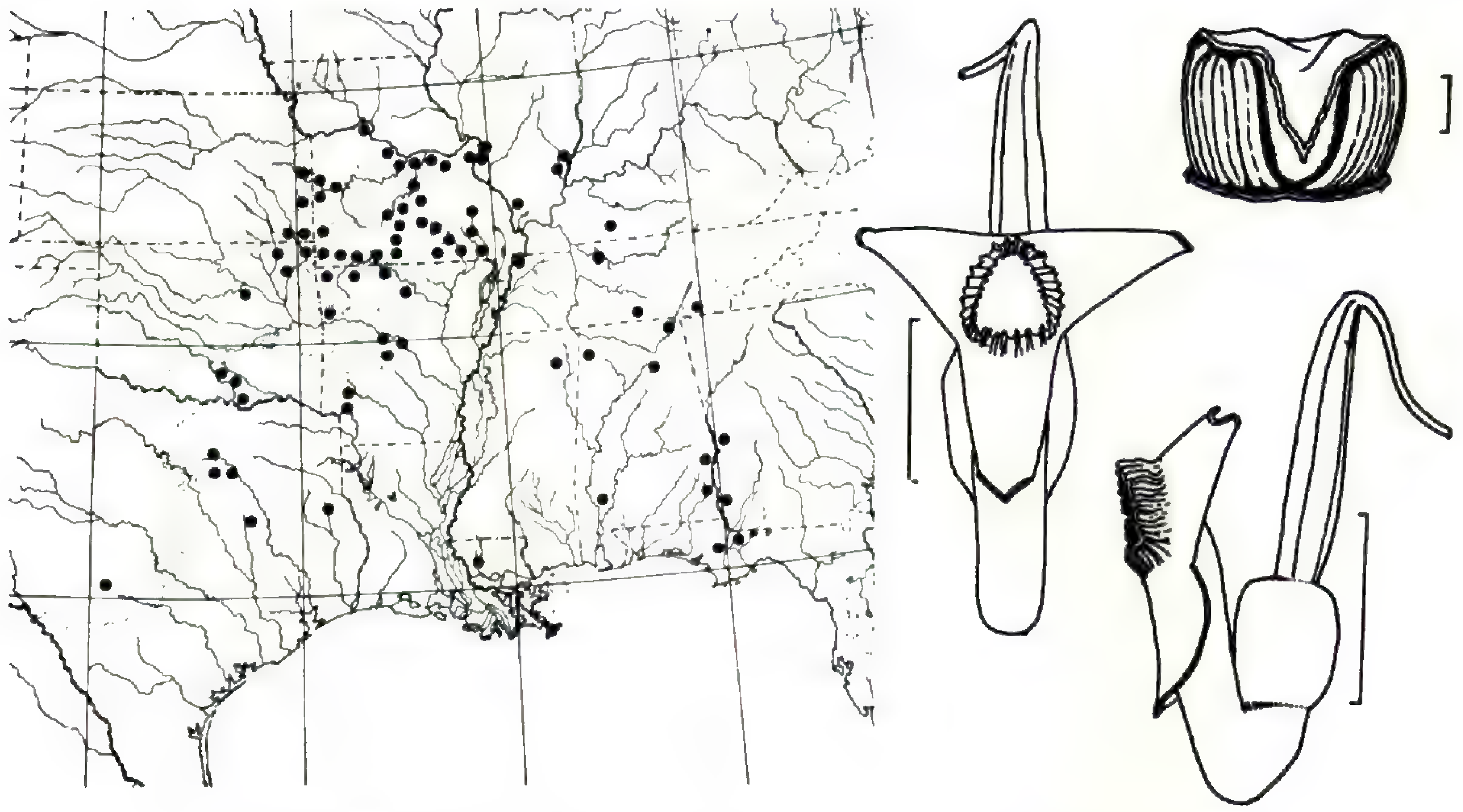


Fig. 16. Distribution, flowers and gynostemium of *A. tomentosa.*

Tomentose *lianas.* *Leaves* broadly cordate, acute to obtuse at the apex, shallowly cordate at the base, 8-15 cm broad, 9-20 cm long, finely pubescent above, beneath tomentose. *Pseudostipules* absent. *Flowers* solitary in the leaf axils, ebracteolate, geniculate, purple, yellow and green, the utricle cylindric, 0.7 cm long, syrinx absent, the tube sharply bent, constricted, 1.5 cm long, the annulus prominent, rugose, the limb smooth, 3-lobed, 2 cm wide, 2 cm long, the lobes convex, strongly revolute, subequal, unappendaged. *Gynostemium* squat, 3-lobed, 3 mm high, 6 mm broad, the anthers 6 in 3 horizontal groups. *Fruits* woody, persistent, finely pubescent, 6-8 cm long, 4-6 cm wide, dehiscence valvate, hypanthium absent. *Seeds* numerous, flat, 1 cm wide, 1 cm long, 1 mm thick.

Mostly in alluvial soils along streams in the southeastern and south-central United States.

UNITED STATES. ALABAMA: Barbour, Blount, Clarke, Franklin, Jackson & Russell counties. ARKANSAS: Benton, Carrol, Crawford, Hempstead, Marion, Perry, Pike, Pulaski, Saline & Stone counties. FLORIDA: Calhoun & Gadsden counties. GEORGIA: Early & Muscogee counties. ILLINOIS: Jackson, Madison, St. Clair, Wabash & White counties. KANSAS: Bourbon, Cherokee, Labette & Miami counties. KENTUCKY: Warren county. LOUISIANA: East Baton Rouge parish. MISSISSIPPI: Lee county. MISSOURI: Barry, Bates, Butler, Carter, Cedar, Cole, Crawford, Douglas, Franklin, Gasconade, Jasper, Laclede, Lincoln, McDonald, Madison, Maries, Miller, Moniteau, Newton, Oregon, Osage, Ozark, Phelps, Pulaski, Ripley, St. Claire, St. Louis, Saline, Shannon, Stone, Taney, Texas, Vernon, Wayne & Wright counties. OKLAHOMA: Bryan, Creek, Johnston, Mayes, Murray, Nowata & Ottawa counties. TENNESSEE: Davidson, Hamilton, Lake & Lincoln counties. TEXAS: Dallas, Denton, Kerr, McLennan, Nacogdoches & Tarrant counties.

Visiting the Smoky Mountain region, one of the areas where the ranges of *A. tomentosa* and *A. macrophylla* abut, I saw neither sympatry nor hybridization; the region of one species ends abruptly where that of the other begins. I know of no satisfactory explanation for this sharp range delineation.

Fig. 17. Distribution, leaf and flower of *A. trilobata.*

15. Aristolochia trilobata L., Sp. Pl. 960, 1753. (Type *Linn. Herb. London, no. 1071.1,* photo)—Fig. 17.

A. 3 scandens P. Browne, Civ. & nat. hist. Jamaica 329, 1756. (ex char.)
A. trifida Lam., Encycl. Méth. Bot. **1:** 251, 1783. (ex char.)
A. triloba Salisb., Prod. 214, 1796. (Based on *A. trilobata* L.)
A. surinamensis Willd., Sp. Pl. **4:** 151, 1805. (ex ic. cit.)
A. macroura Gomez, Mem. Acad. Lisboa **3:** Mem. dos Corresp. 77, 1812. (Type: *Martius inter Brasil 1817,* photo M)
A. appendiculata Vell., Fl. Flum. **9:** *t. 98,* 1827. (ex ic.)
A. caudata Booth ex Lindl., Bot. Reg. *t. 1453,* 1831, non Jacq. (1762), nec Parodi (1878). (ex ic.)
A. macrota Duchr. in DC., Prod. **15** (1): 447, 1864. (Type: *Schomburgk 679,* photo G-DC.)
A. tapetotricha Lem., Illustr. Hortic. **3:** Misc. 22, 1856. (ex char.)
Howardia macroura (Gomez) Klotzsch, Monatsb. Acad. Berlin **1859:** 617, 1859.
H. surinamensis (Willd.) Klotzsch, loc. cit. 613.
H. trilobata (L.) Klotzsch, loc. cit. 617.

Glabrous, strong *lianas. Leaves* deeply to barely palmately 3-lobed, truncate at the base, 3-15 cm broad, 10-15 cm long. *Pseudostipules* suborbiculate, amplexicaul. *Flowers* solitary in the leaf axils, ebracteolate, geniculate, the utricle ellipsoid, 4-5 cm long, syrinx absent, the tube bent, 5-7 cm long, annulus absent, the limb smooth, 1-lobed, (the tube and limb resembling the pitcher and lid of a *Sarracenia*), narrowly triangular, 2-3 cm wide, 15-20 cm long, including the length of the tape-like appendix. *Gynostemium* 6-lobed, 7 mm high, 6 mm broad, the anthers 6, equidistant. *Fruits* cylindric, 9 cm long, 2.5 cm wide, dehiscence acropetal, septifragal, the hypanthium absent. *Seeds* numerous, flat, triangular, 8 mm wide, 8 mm long, 1 mm thick.

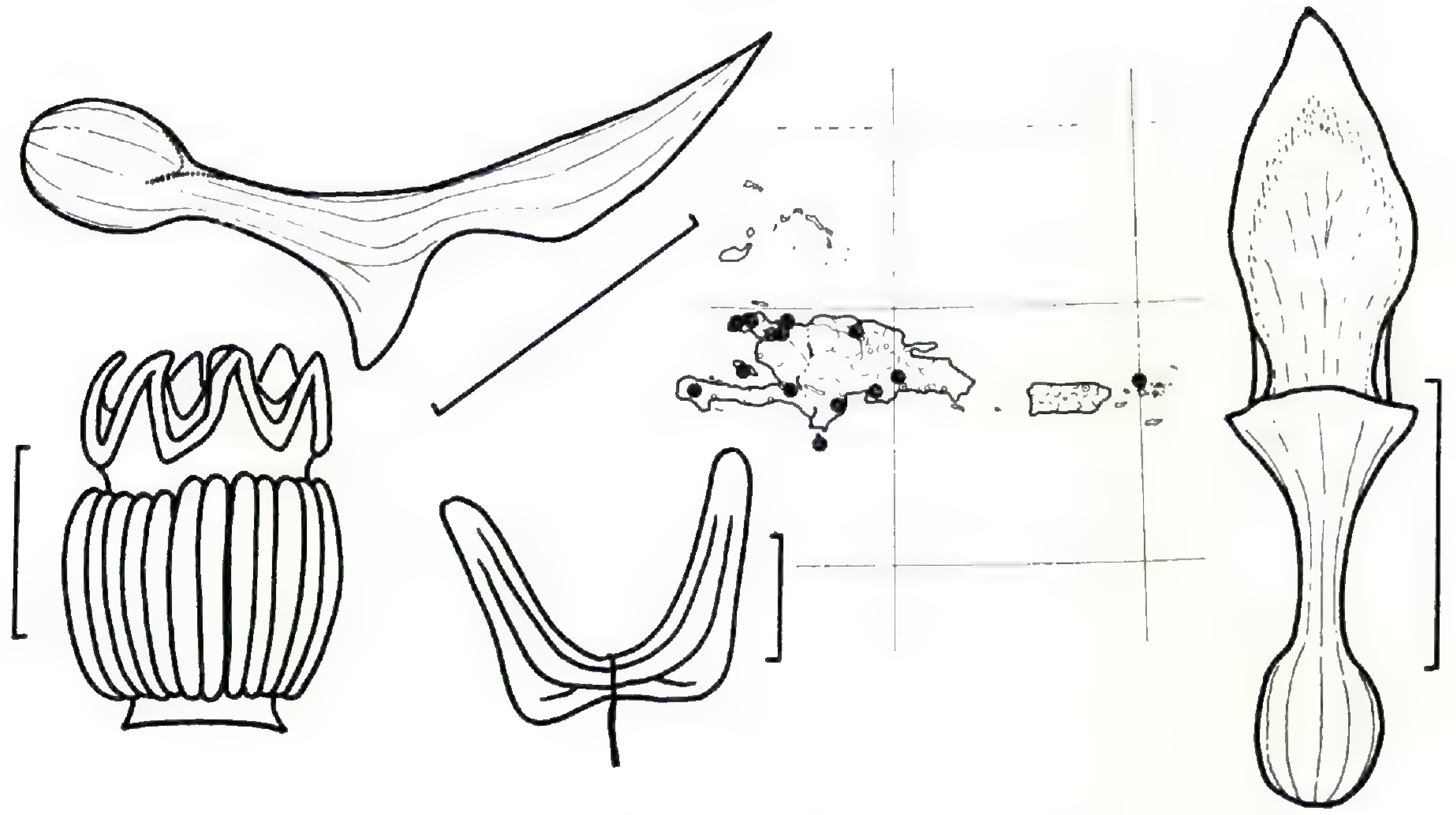


Fig. 18. Gynostemium, leaf, flowers and distribution of *A. bilobata.*

At clearing margins, in thickets and woodlands, along the Caribbean side of Central America from British Honduras to Panama, and throughout the West Indies.

British Honduras: Belize, Monkey River, Stann Creek.
Honduras: Atlántida.
Costa Rica: Limón.
Panama: Canal Zone, Chiriquí.
Bermuda. Cuba: Oriente. Jamaica. Haiti. Dominican Repubic. Puerto Rico. St. Thomas. Tortola. Antigua. Guadeloupe. Dominica. Martinique. St. Vincent. Trinidad.

16. Aristolochia bilobata L., Sp. Pl. 960, 1753. (ex ic. cit.)—Fig. 18.

Tropexa biloba Raf., Fl. Tellur. **4:** 98, 1838. (Based on *A. bilobata* L.)
Howardia bilobata (L.) Klotzsch, Monatsb. Acad. Berlin **1859:** 619, 1859.

Glabrous small *lianas. Leaves* palmately 2-lobed, truncate at the base, 1-3 cm broad 1-2.5 cm long. *Pseudostipules* absent. *Flowers* solitary in the leaf axils, ebracteolate, rectilinear, purple, the utricle ellipsoid, 5-8 mm long, syrinx an inequilateral cylinder, the tube straight, 5-10 mm long, the limb smoth, 1-lobed, lanceolate, exappendiculate, 6-10 cm wide, 15-22 mm long. *Gynostemium* 6-lobed, 2 mm high, 2 mm broad, the anthers 6, equidistant. *Fruits* short-cylindric, 2.5 cm long, 1.5 cm wide, dehiscence acropetal, septifragal, the hypanthium 2-3 mm long. *Seeds* numerous, flat, 5 mm wide, 6 mm long, 0.2 mm thick.

On low bushes and in thickets in dry soils on the islands of Hispaniola and St. Thomas, and other smaller islands nearby.

Haiti (incl. Gonave I.). Dominican Republic (incl. Beata I.). St. Thomas.

While this species is frequently collected without flowers or fruits, it can be readily identified by the curious bilobate leaves.

17. Aristolochia lindeniana Duchr. in DC., Prod. **15**-1: 453, 1864. (Type: *Linden 18*, not seen)—Fig. 19.

A. lindeniana Duchr. var. *plagiophylla* Griseb., Cat. Pl. Cub. 115, 1866. (Type: *Wright 2616*, MO)
A. clementis Alain, Rev. Soc. Cubana Bot. **5**: 80, 1948. (Type: *Clemente 6096*, NY)

Small, twiggy *lianas*. *Leaves* varying widely in size, strongly oblate-reniform, shallowly emarginate, rarely truncate at the apex, basally subtruncate, peltate, 17-25 mm broad, 5-9 mm long, smooth above and beneath, green. *Pseudostipules* absent. *Flowers* solitary in the leaf axils, ebracteolate, geniculate, terra cotta and purple, the utricle ovoid, 1 cm long, syrinx absent, the tube bent, 5 mm long, the limb 1-lobed, smooth, ovate, the margins crisped, revolute, 8 mm wide, 13 mm long, unappendaged. *Gynostemium* 6-lobed, 2 mm high, 2 mm broad, the anthers 6, equidistant. *Fruits* small, spheric, 8 mm diameter, the hypanthium straight, 2 mm long. *Seeds* numerous, flat, 3 mm wide, 3 mm long, 0.5 mm thick.

In dry limestone and pine forests, eastern Cuba.

Cuba: Oriente.

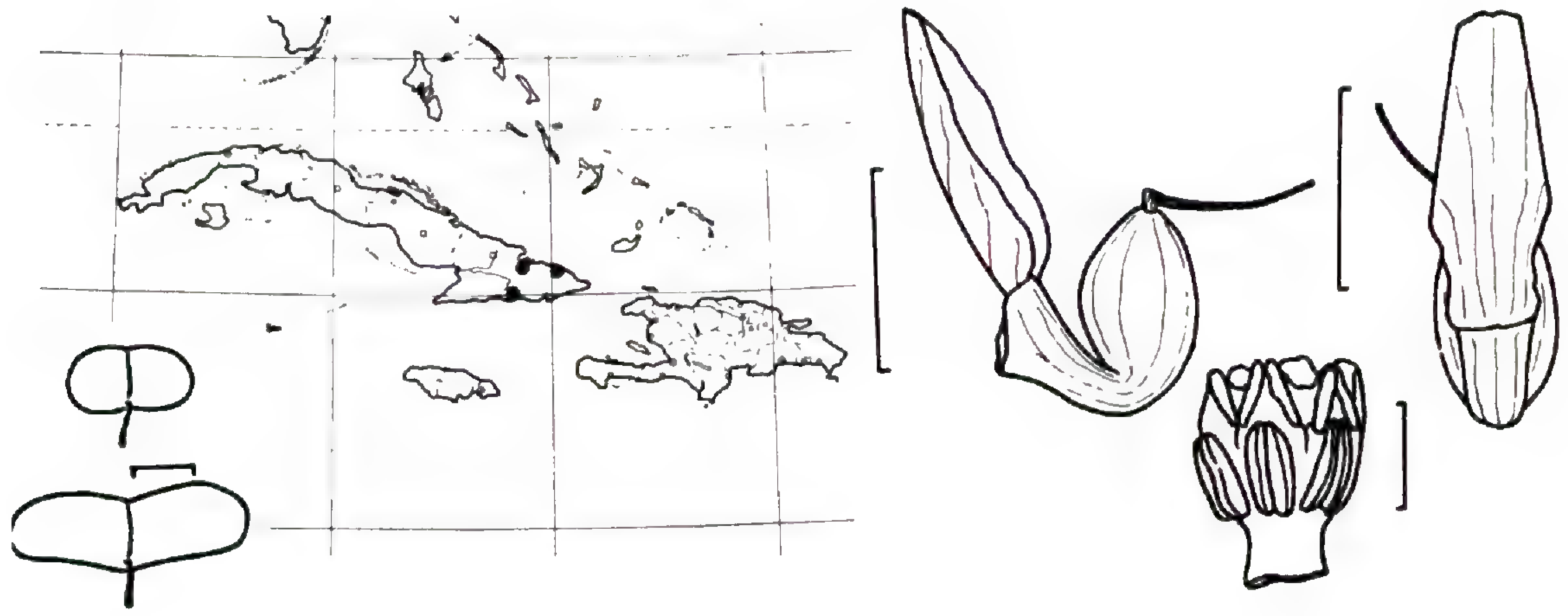


Fig. 19. Leaves, distribution, flowers and gynostemium of *A. lindeniana*.

18. Aristolochia peltata L., Sp. Pl. 960, 1753. (ex char.)—Fig. 20.

A. reniformis Willd., Sp. Pl. **4**: 153, 1805, non Vell. (1827). (ex char.)
Howardia peltata (L.) Klotzsch, Monatsb. Acad. Berlin **1859**: 618, 1859.
H. reniformis (Willd.) Klotzsch, loc. cit.

Subglabrous *lianas*. *Leaves* strongly oblate-reniform, emarginate, cordate, barely peltate, 3-4 cm broad, 1.5-2.2 cm long, minutely hamate-hairy above, beneath glabrous. *Pseudostipules* absent. *Flowers* solitary in the leaf axils, ebracteolate, rectilinear, purple and green, the utricle ovoid, 8-10 mm long, syrinx small, inequilateral, the tube straight or slightly arcuate, 1.5-2.0 cm long, the limb 1-lobed, long-spatulate, densely fimbriate on the expanded terminal portion, ca 6 cm long, the apex obtuse to emarginate. *Gynostemium* 6-lobed, 2 mm high, 2 mm broad, the anthers 6, equidistant. *Fruits* short-cylindric, 2 cm long, 1.3 cm wide, dehiscence

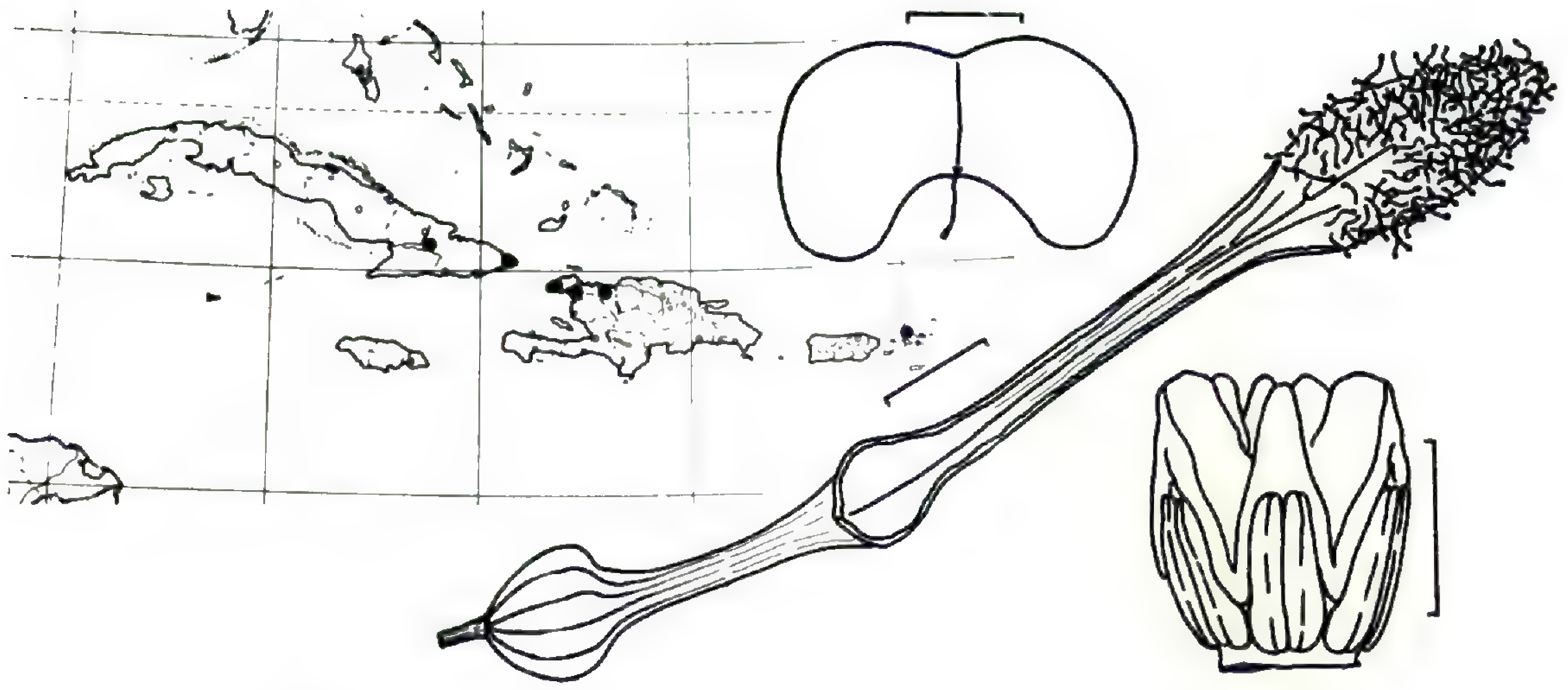


Fig. 20. Distribution, leaf, flower and gynostemium of *A. peltata.*

acropetal, septifragal, the hypanthium 2 mm long. *Seeds* numerous, flat, 4 mm wide, 3.5 mm long, 0.2 mm thick.

On shrubs, in dry thickets, eastern Cuba, Haiti and St. Thomas.

CUBA: Oriente. HAITI. ST. THOMAS.

The curious, long limb is densely fimbriate on the expanded terminal lobe and has no prominent warts or tubercles; this will differentiate *A. peltata* from *A. fuertesii.*

19. ARISTOLOCHIA LEPTOSTICTA Urban, Symb. Antill. **7:** 206, 1912. (Type: *von Tuerckheim 2661,* not seen)—Fig. 21.

A. peltata L. var. *poitaei* Urban, loc. cit. 207. (Type: *Bredemeyer* 17054, not seen)

Glabrous *lianas. Leaves* strongly oblate-reniform, obtuse at the apex, apiculate, basally cordate-hastate, 2.5-4.0 cm broad, 2.5-4.0 cm long, glabrous, smooth.

Fig. 21. Distribution, flower, gynostemium and leaf of *A. leptosticta.*

Pseudostipules absent. *Flowers* solitary in the leaf axils, ebracteolate, rectilinear, yellow and spotted purple, the utricle ovoid, 7 mm long, syrinx a low cylindric rim, the tube straight, 7 mm long, the limb 1-lobed, fimbriate-warty, ovate-spatulate, 8 mm wide, 1.5 cm long, unappendaged. *Gynostemium* 6-lobed, squat, 2 mm high, 3 mm broad, the anthers 6, equidistant. *Fruits* not seen.

In thickets and dry limestone rocks, along the southern shores of Hispaniola.

Haiti. Dominican Republic.

While I have not seen Urban's type, he listed two other collections in addition to the holotype. My identification is based upon both of these, *Fuertes 26* (US) and *Fuertes 973b* (A).

20. Aristolochia haitiensis Ekman & Schmidt in Fedde, Repert. Sp. Nov. **27:** 101, 1929. (Type: *Ekman H8671*, S, US)—Fig. 22.

Glabrous, twiggy *lianas*. *Leaves* strongly oblate reniform, subrectangular, emarginate, basally truncate, barely subpeltate, 2-2.5 cm broad, 7-9 mm long, green, smooth. *Pseudostipules* absent. *Flowers* solitary in the leaf axils, ebracteolate, rectilinear, spotted purple, the utricle ovoid, 6-8 mm long, syrinx a small, inequilateral flap, the tube straight, 8-12 mm long, the limb 1-lobed, fimbriate-warty, spatulate, 7-9 mm wide, 15 mm long, unappendaged. *Gynostemium* 6-lobed, 2 mm high, 2 mm broad, the anthers 6, equidistant. *Fruits* small, cylindric, 1.75 cm long, 0.75 cm wide, dehiscence acropetal, septifragal, the hypanthium slightly curved, 3 mm long. *Seeds* numerous, flat, 2.5 mm wide, 3 mm long, 0.2 mm thick.

On limestone rocks; known only from islands in Golfe de la Gonave.

Haiti.

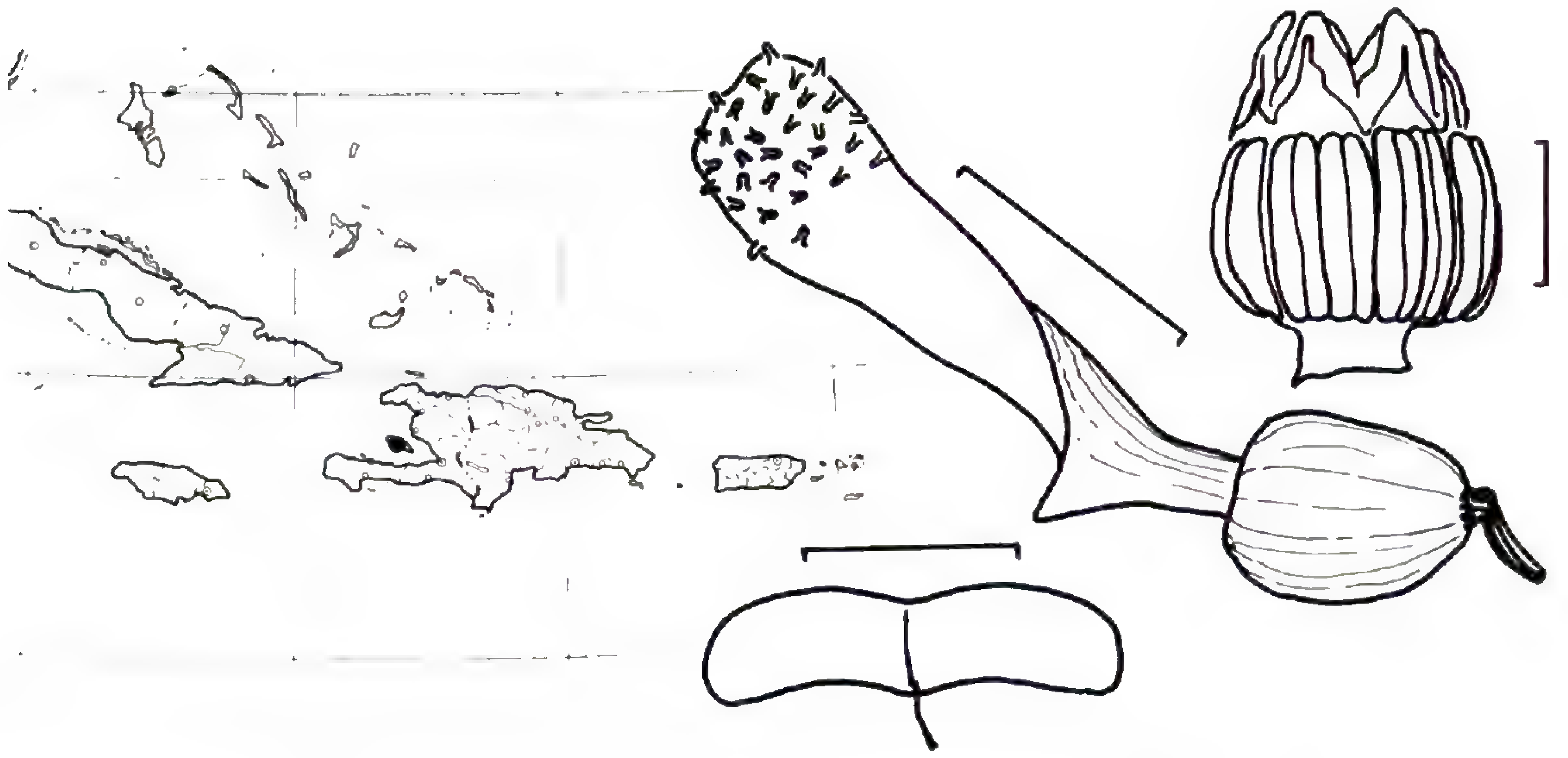


Fig. 22. Distribution, leaf, flower and gynostemium of *A. haitiensis*.

21. ARISTOLOCHIA TENTACULATA Schmidt in Fedde, Repert. Sp. Nov. **23:** 283, 1927. (Type: *Palmer 351,* A, F, GH, MO, NY, UC, US)—Fig. 23.

Glabrous small *lianas*... *Leaves* cordate-orbiculate, slightly emarginate, cordate-auriculate, 2-6 cm broad, 3-8 cm long, smooth above, beneath paler with emersed veins. *Pseudostipules* absent. *Flowers* solitary in the leaf axils, often on small-leafed, short, lateral shoots, ebracteolate, subgeniculate, purple, green and yellow, the utricle gibbous-obconic, 1 cm long, syrinx inequilateral, annular, the tube straight, narrow at first, thence flaring into the limb, 2-3 cm long, the limb broadly lanceolate, sparsely long-fimbriate along the lateral margins, 2.5 cm wide, 6-8 cm long, unappendaged. *Gynostemium* 6-lobed, 4 mm high, 4-5 mm broad, the anthers 6, equidistant. *Fruits* cylindric, 5 cm long, 2.5 cm wide, dehiscence acropetal, septifragal, the hypanthium straight, 2 mm long. *Seeds* numerous, 6.5 mm wide, 8 mm long, thin, papery.

On shrubs and in open woodlands, west-central Mexico.

MEXICO: Guerrero, Mexico, Michoacán.

This species, called *guaco* (along with most other Mexican species of *Aristolochia*) by the native population, is used by Mexicans for treating nearly every chronic constitutional disorder of man.

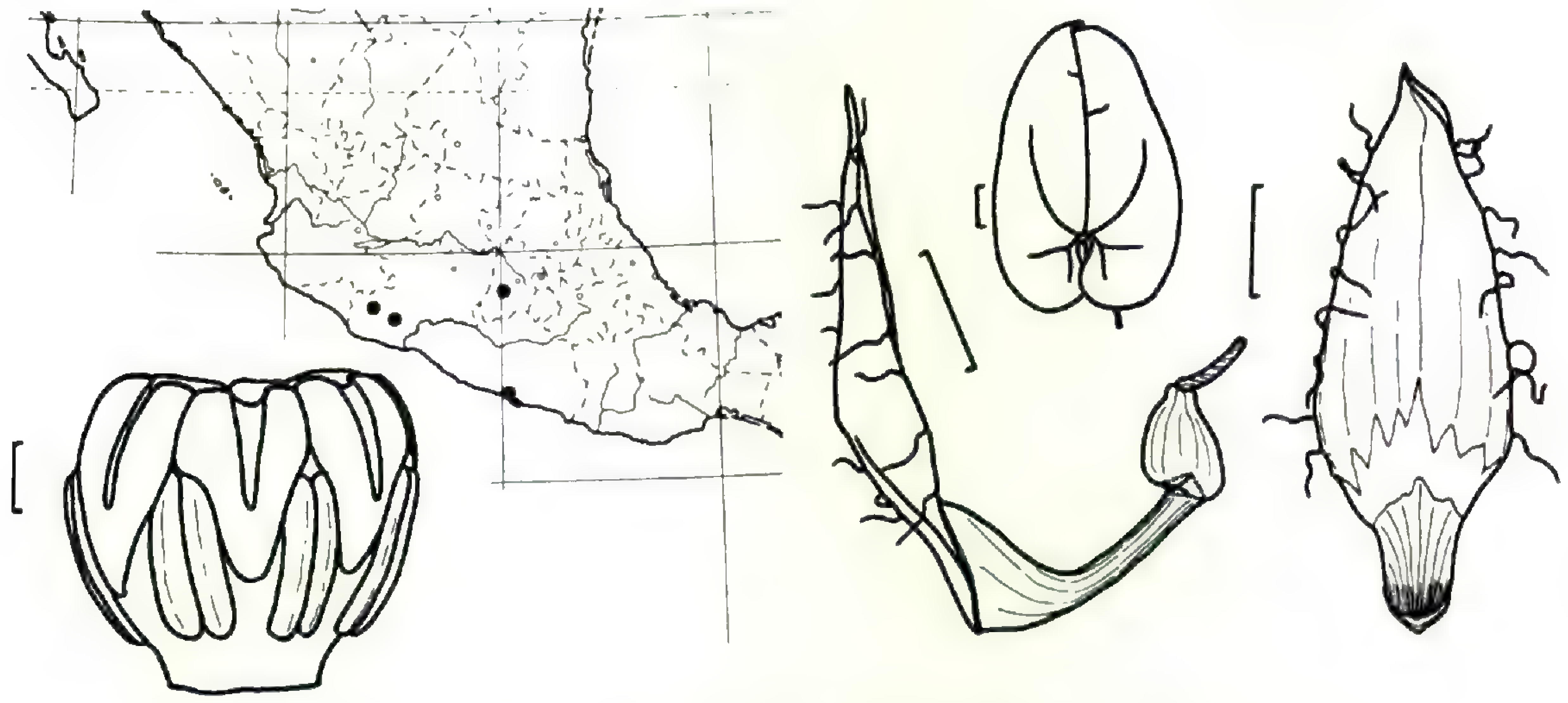


Fig. 23. Gynostemium, distribution, flowers and leaf of *A. tentaculata.*

22. ARISTOLOCHIA PILOSA H.B.K., Nov. Gen. Sp. Pl. **2:** 146, *t. 113,* 1817. (ex ic.)—Fig. 24.

Howardia pilosa (H.B.K.) Klotzsch, Monatsb. Acad. Berlin **1859:** 612, 1859.
H. costaricensis Klotzsch, loc. cit. 614. (Type: *Hoffman s.n.,* photo G-DC)
Aristolochia costaricensis (Klotzsch) Duchr. in DC., Prod. **15**(1): 450, 1864.
A. pilosa H.B.K. var. *ligulifera* Mast., Bot. Gaz. **33:** 256, 1902. (Type: *von Tuerckheim* (JDS) *7768,* A, GH, NY, US)
A. ferruginea Brandg., Univ. Calif. Pub. Bot. **6**:51, 1914. (Type: *Purpus 6931,* F, GH, MO, NY, UC, US)
A. haughtiana Hoehne, Arquiv. Bot. Estad. S. Paulo, n. s., **2:** 99, *t.* 37, 1947. (Type: *Haught 4648,* US)

Hispid-pilose *lianas. Leaves* oval to ovate, acute at the apex, basally deeply

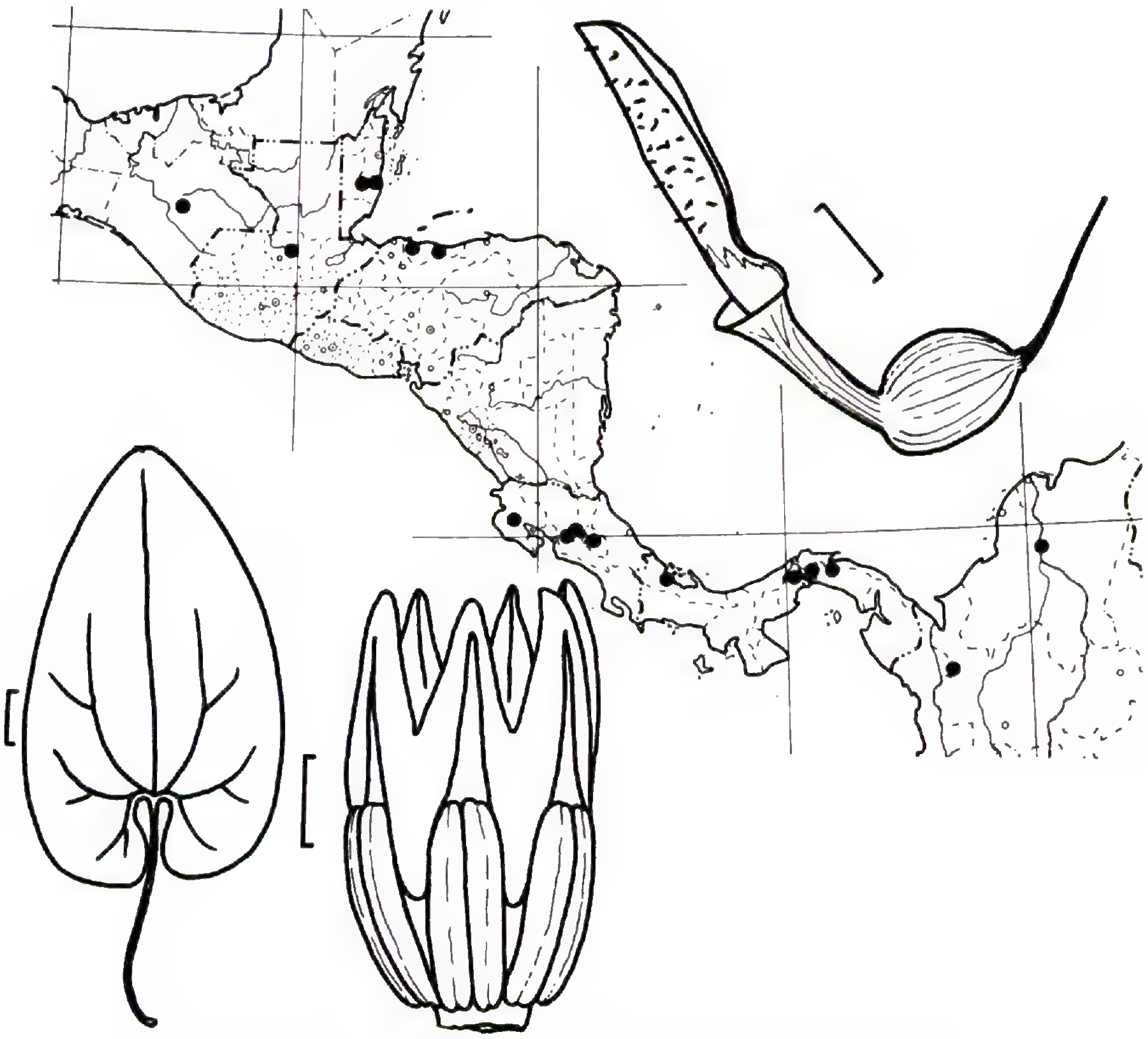


Fig. 24. Leaf, gynostemium, distribution and flower of *A. pilosa*.

cordate, 5-10 cm broad, 6-15 cm long, deep green, glabrescent above, beneath paler, pilose along the veins. *Pseudostipules* absent. *Flowers* solitary in the leaf axils, ebracteolate, arcuate, purple, green and yellow, the utricle ovoid, 1.5 cm long, syrinx inequilateral, small, annular, the tube straight, 1.5-2.5 cm long, the limb 1-lobed, sparsely to heavily fimbriate, lingulate-spatulate, 2 cm wide, 3.5-4.5 cm long, unappendaged. *Gynostemium* 6-lobed, 5 mm high, 3 mm broad, the anthers 6, equidistant. *Fruits* large, woody, short-cylindric, 6-7 cm long, 4-5 cm wide, dehiscence acropetal, septifragal, the hypanthium absent. *Seeds* numerous, flat, 15 mm wide, 11 mm long, 1 mm thick.

Rain forests, southern Mexico to Colombia in our area; probably extensively distributed in South America.

Mexico: Chiapas.
Guatemala: Alta Verapaz.
British Honduras: Belice.
Honduras: Atlántida.
Costa Rica: Alajuela, Cartago, Guanacaste.
Panama: Canal Zone, Chiriquí, Panama.

This is the only conspicuously stiff-haired hexandrous species in our area. Authors have treated fimbriate plants as *A. costaricensis*, and efimbriate ones as *A.*

pilosa, but many intermediates occur which are indistinguishable from one another in other details; the intermediates, furthermore, do not occur in any geographic sequence.

23. Aristolochia taliscana Hook. & Arn., Bot. Beech. Voy. 309, 1840. (Type: *Lay & Collie s.n.*, BM)—Fig. 25.

A. galeottii Duchr., Ann. Sci. Nat., sér. 4, **2:** 44, 1854. (Type: *Galeotti 212*, P; photos F, MO)
A. pardina Duchr., loc. cit. 47. (Type: *Ghiesbreght 214*, F, P)

Glabrescent *lianas*. *Leaves* broadly cordate, rounded to emarginate, basally deeply cordate-auriculate, 2.5-6.0 cm broad, 2.5-7.0 cm long, smooth. *Pseudostipules* absent. *Flowers* solitary in the leaf axils, slightly arcuate to sharply geniculate, brown and yellow, the utricle obconic, 8 mm long, syrinx inequilateral, annular, the tube straight, 2-3 cm long, the limb subspatulate, erect, densely to sparsely fimbriate-warty, fimbriae variable, small and few to large and numerous, 1 cm wide, 2.5-3.0 cm long, unappendaged. *Gynostemium* 6-lobed, 2.5-3.5 mm high, 2-4 mm broad, the anthers 6, equidistant. *Fruits* cylindric, 3.5 cm long, 2.0-2.5 cm wide, dehiscence acropetal, septifragal, the hypanthium slightly curved, 4 mm long. *Seeds* numerous, flat, 6 mm wide, 9 mm long, 0.5 mm thick.

In thickets, open places and scrub forests, west-central Mexico.

Mexico: Colima, María Madre I., Michoacán, Nayarit, Sinaloa.

This species is one of the most variable, and thus confusing, of all the species treated in this paper. There are several extremes of flower structure, and all intermingle and merge in various combinations. Placing all of these variants in a single species perhaps is not adequate treatment, but any other action is precluded without extensive field studies.

A word might be added regarding the spelling of the species epithet. It was named for Jalisco, but regretably was published as *taliscana*. While a correction would satisfy a few overmeticulous persons, there is little need to litter *Aristolochia* with yet another name. I choose to allow it to remain as *taliscana*.

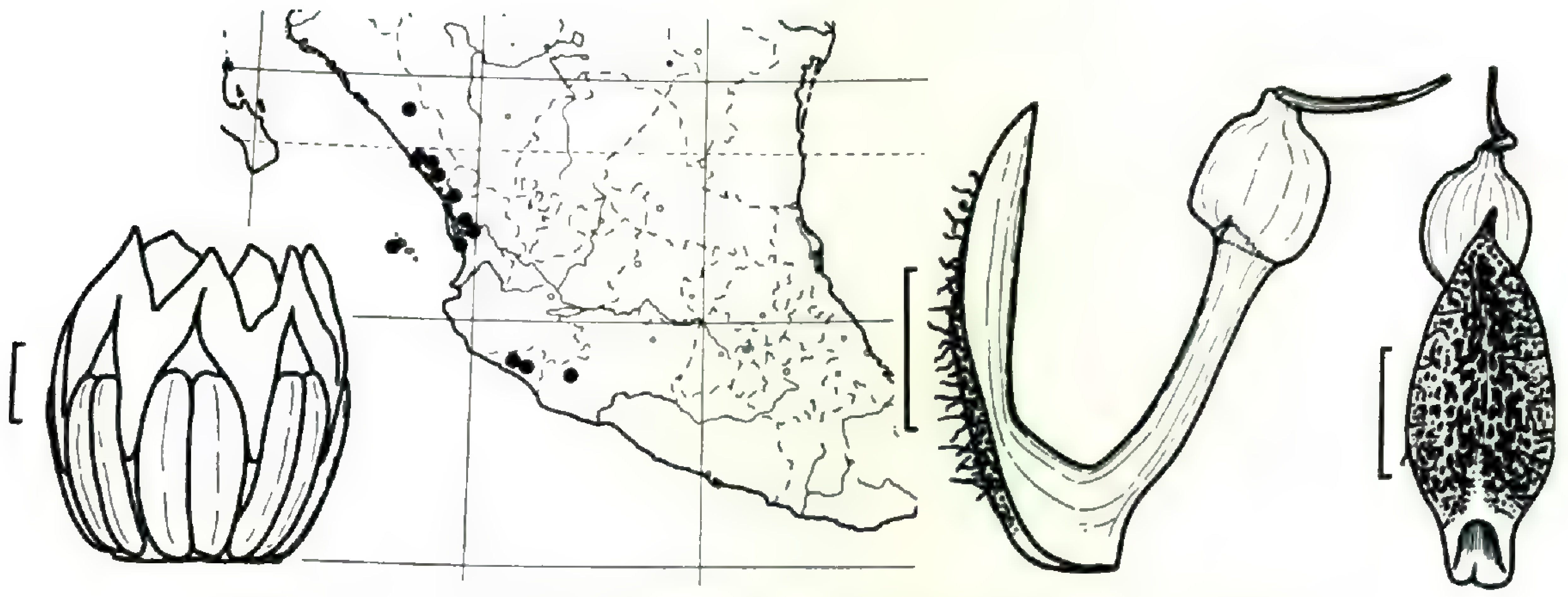


Fig. 25. Gynostemium, distribution and flowers of *A. taliscana*.

24. Aristolochia glandulosa Kickx, Bull. Acad. Roy. Brux., **1839:** 453, *t. 455,* 1839. (ex ic. cit.)—Fig. 26.

A. macradenia Hook., Bot. Mag. *t. 4467,* 1849. (ex ic. cit.)
Howardia macradenia (Hook). Klotzsch, Monatsb. Acad. Berlin **1859:** 618, 1859.
Aristolochia glandulosa Kickx *β glabra* Duchr. in DC., Prod. **15**(1): 452, 1864. (Based on *A. macradenia* Hook.)

Finely tomentulose *lianas. Leaves* broadly to narrowly pandurate, medially constricted, slightly emarginate to obtuse, deeply cordate-hastate, 2.5-6.0 cm broad, 7.5-12.0 cm long, deep green, finely hamate-hairy above, often therefore scabrous, beneath delicately tomentulose. *Pseudostipules* absent. *Flowers* solitary in the leaf axils, ebracteolate, rectilinear to subarcuate, green and dark purple, the utricle ovoid, 1.5 cm long, syrinx a small rim, the tube straight, ca 2 cm long, the limb 1-lobed, ovate, with peltate-capitate fimbriae, 2-2.5 cm wide, 3-4 cm long, unappendaged. *Gynostemium* 6-lobed, obconic, 5 mm high, 3 mm broad, the anthers 6, equidistant. *Fruits* cylindric, pubescent, 4 cm long, 2.5 cm wide, dehiscence acropetal, septifragal, the hypanthium absent. *Seeds* numerous, flat, 7 mm wide, 7 mm long, 0.5 mm thick.

Climbing on shrubs and rocks in limestone soils, western Cuba.

Cuba: Habana, Isla de Pinos, Pinár del Río, Santa Clara.

The curious fimbriae distinguish *A. glandulosa* sufficiently well. It is also noteworthy for the strange, scabrous leaves, a condition also seen in a few other species, but most striking here and due to the presence of great numbers of minute, hamate hairs on the upper surfaces of the leaves.

Fig. 26. Flowers, leaf, distribution and gynostemium of *A. glandulosa*.

25. Aristolochia clavidenia Griseb., Cat. Pl. Cub. 115, 1866. (Type: *Wright 2612,* MO, NY)—Fig. 27.

Glabrescent *lianas. Leaves* broadly to narrowly pandurate, medially constricted, obtuse at the apex, basally cordate-hastate, 6-12 cm broad, 7-14 cm long, dark

green and smooth above, beneath paler, sparsely very fine-puberulent. *Pseudostipules* absent. *Flowers* solitary in the leaf axils, ebracteolate, subgeniculate, purplish, the utricle obconic, 1.5 cm long, syrinx inequilateral, annular, the tube arched, 2 cm long, the limb 1-lobed, spatulate, the terminal portion with laterally compressed capitate fimbriae, 2 cm wide, 4-6 cm long. *Gynostemium* 6-lobed, 5 mm high, 4 mm broad, the anthers 6, equidistant. *Fruits* not seen.

Habitat not known, eastern Cuba.

CUBA: Oriente.

Aristolochia clavidenia is distinguishable from all other species by the laterally compressed, capitate fimbriae and the large flowers.

26. ARISTOLOCHIA FUERTESII Urban, Symb. Antill. **7**: 207, 1912. (Type: *Fuertes 902,* A)—Fig. 28.

Puberulent, glabrescent *lianas*. *Leaves* broadly to narrowly pandurate, medially constricted, obtuse to emarginate, broadly and deeply cordate-hastate, 17-22 mm broad, 17-24 mm long, smooth above, beneath slightly paler, puberulent. *Pseudostipules* absent. *Flowers* solitary in the leaf axils, ebracteolate, 6 mm long, syrinx an inequilateral flap, the tube straight, 17-22 mm long, the limb 1-lobed, long-spatulate, with fimbriae subulate, chiefly marginal, large, warty, the limb apex emarginate, 7 mm wide, 27-30 mm long overall. *Gynostemium* 6-lobed, 1.4 mm high, 1.2 mm broad, the anthers 6, equidistant. *Fruits* not seen.

In dry thickets, extreme southern Hispaniola.

HAITI. DOMINICAN REPUBLIC.

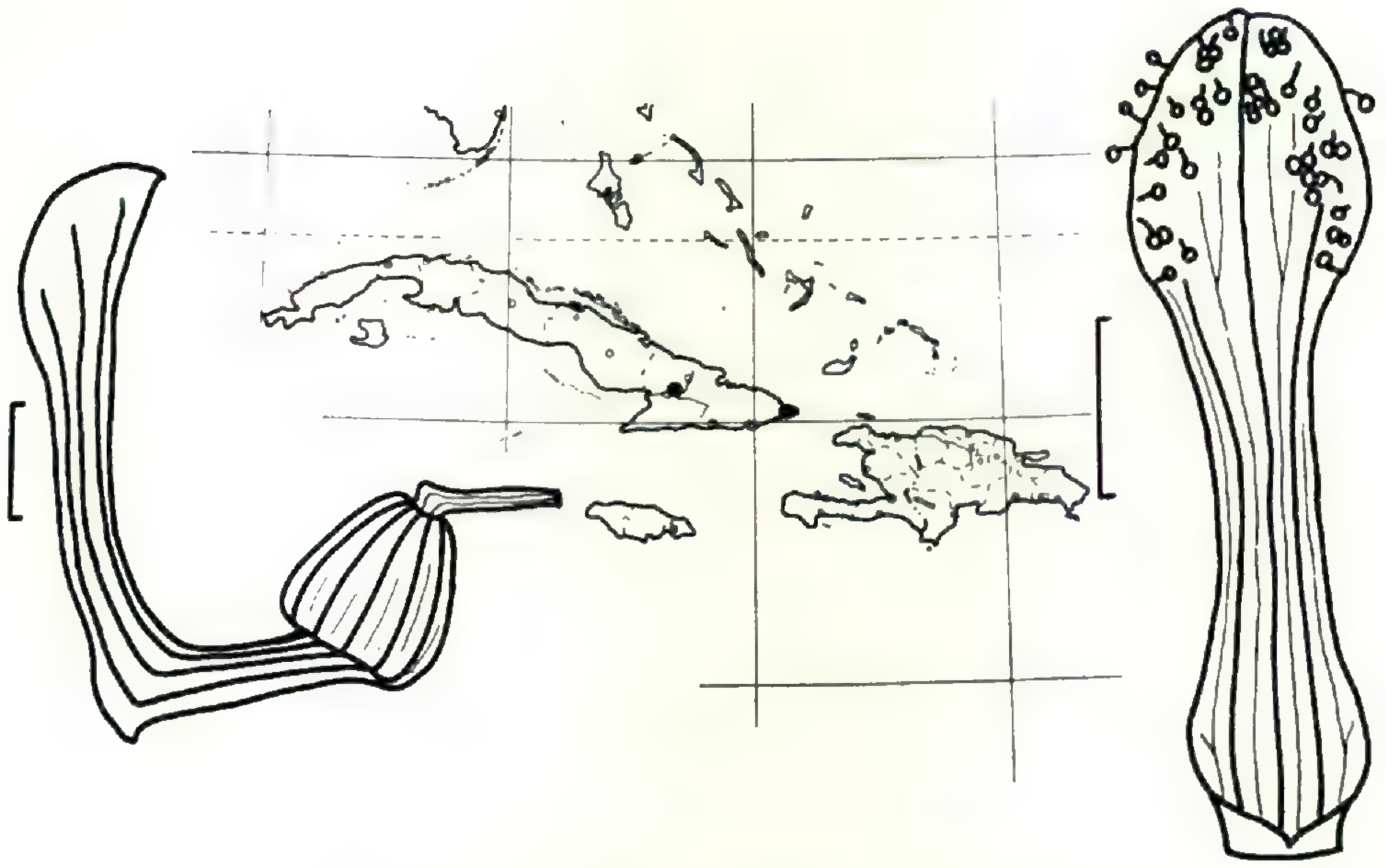


Fig. 27. Flowers and distribution of *A. clavidenia*.

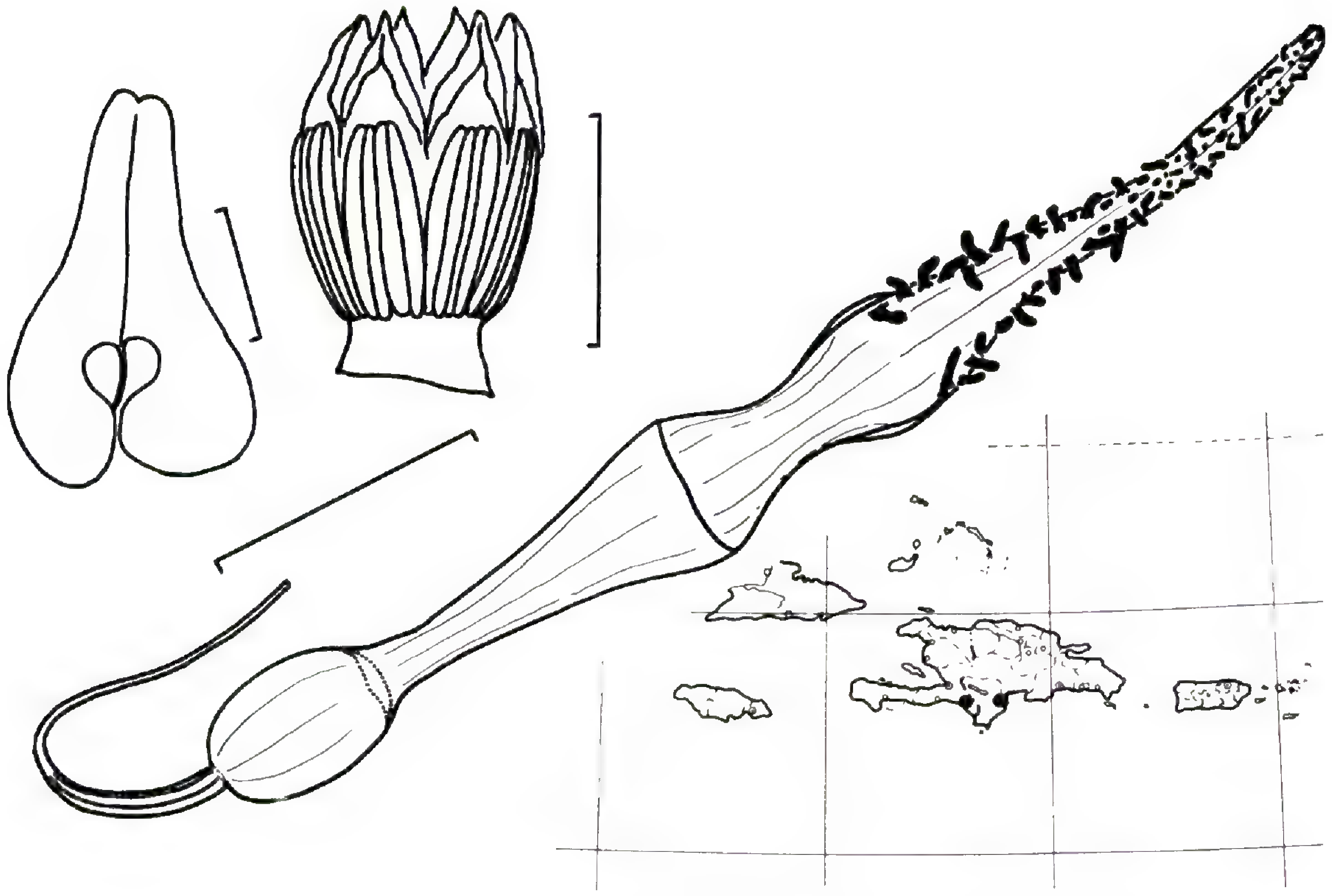


Fig. 28. Leaf, gynostemium, flower and distribution of *A. fuertesii.*

27. Aristolochia rugosa Lam., Encycl. Méth. Bot. **1:** 252, 1783. (ex ic. cit.)—Fig. 29.

A. obtusata Sw., Prod. Veg. Ind. Occ. 126, 1788. (ex ic. cit.)
A. barbata Jacq., Ic. Pl. Rar. **3:** *t. 608,* 1789. (ex ic.)
A. dictyantha Duchr., Ann. Sci. Nat., sér. 4, **2:** 40, 1854. (Type: *Vargas s.n.*, photo G-DC)
A. eurystoma Duchr., loc. cit. 41. (Type: *Beaupertuis s.n.*, P)
Howardia obtusata (Sw.) Klotzsch, Monatsb. Acad. Berlin **1859:** 612, 1859.
H. barbata (Jacq.) Klotzsch, loc. cit. 613.
H. schomburgkii Klotzsch, loc. cit. (ex char.)
Aristolochia dictyantha Duchr. *β schomburgkii* (Klotzsch) Duchr. in DC., Prod. **15**(1): 447, 1864.
A. rumicifolia Schomb. ex Duchr., loc. cit., non Mart. (1824), pro syn.

Glabrescent *lianas. Leaves* broadly to narrowly pandurate, medially constricted, with rounded apices, the bases deeply cordate-sagittate, 3-7 cm broad, 8-12 cm long, paler beneath. *Pseudostipules* absent. *Flowers* solitary, axillary, ebracteolate, rectilinear, the utricle subovoid, 1 cm long, syrinx an inequilateral flap, the tube trumpet-shaped, straight, 3 cm long, the limb 1-lobed, broadly spatulate, with subulate, surficial fimbriae, 1 cm wide, 1.5-2.0 cm long. *Gynostemium* coroniform, 6-lobed, the anthers 6, equidistant. *Fruits* cylindric, 5 cm long, 1.5 cm wide, dehiscence neither acropetal nor basipetal, but appearing median, septifragal. *Seeds* numerous, subrevolute, 4 mm wide, 5 mm long, 1 mm thick.

Apparently limited in our range to the Leeward Islands.

Antigua. Guadeloupe. Martinique.

The dehiscence type of the fruits of *A. rugosa* is intermediate between two well-defined extremes, acropetal and basipetal. The papery consistency of the

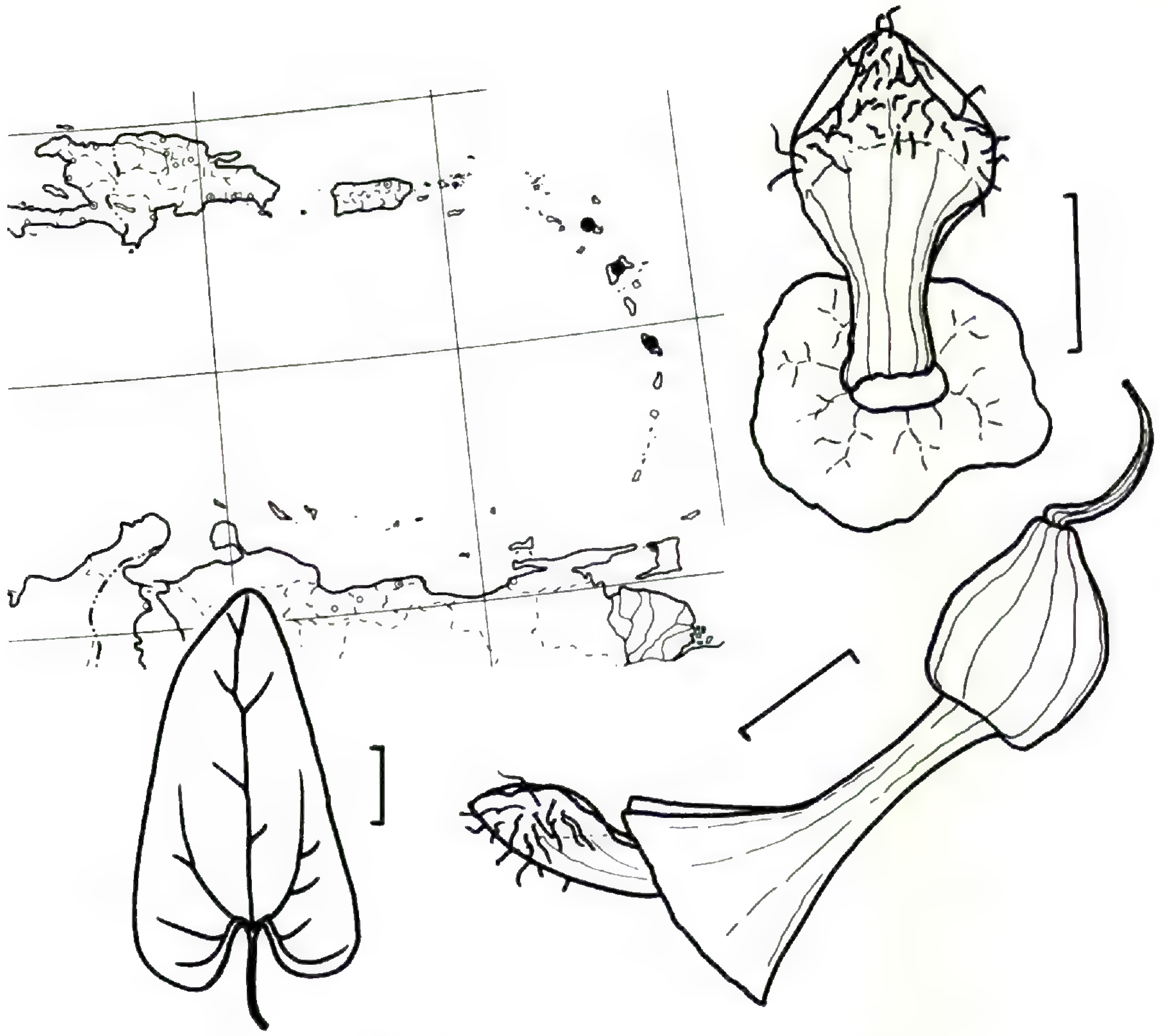


Fig. 29. Distribution, leaf and flowers of *A. rugosa*.

capsules seems to reflect closer affinities with those of acropetal dehiscence, but the subrevolute seeds are typical of the basipetally opening fruits.

28. Aristolochia passifloraefolia A. Rich., Fl. Cub. Fanerog. **2:** 195, 1850. (Type: *Sagra s.n.*, P)—Fig. 30.

A. cyclochilia Duchr., Ann. Sci. Nat., sér. 4, **2:** 45, 1854. (Type: *Sagra s.n.*, not seen)
A. trichostoma Griseb., Mem. Amer. Acad., n. s., **8:** 190, 1861. (Type: *Wright 463,* MO, P)
A. spathulata Duchr. in DC., Prod. **15**(1):448, 1864. (Type: *Wright 463,* MO, P)

Glabrescent *lianas. Leaves* heteromorphic, subtriangular, or broadly to narrowly pandurate, medially constricted, acuminate to obtuse at the apex, basally sagittate-auriculate to cordate to auriculate-hastate, 2-6 cm broad, 4-10 cm long, smooth. *Pseudostipules* absent. *Flowers* solitary in the leaf axils, ebracteolate, subgeniculate, purple marked with green, the utricle ovoid, ca 1 cm long, syrinx inequilateral, small, the tube straight to arcuate, 1-1.5 cm long, the limb 1-lobed, broadly spatulate, densely subulate-fimbriate, 1 cm wide, 2-3 cm long, unappendaged. *Gynostemium* 6-lobed, 2-3 mm high, 2 mm broad, the anthers 6, equidistant. *Fruits* cylindric 3.5-4.0 cm long, 2.0-2.5 cm wide, dehiscing acropetally,

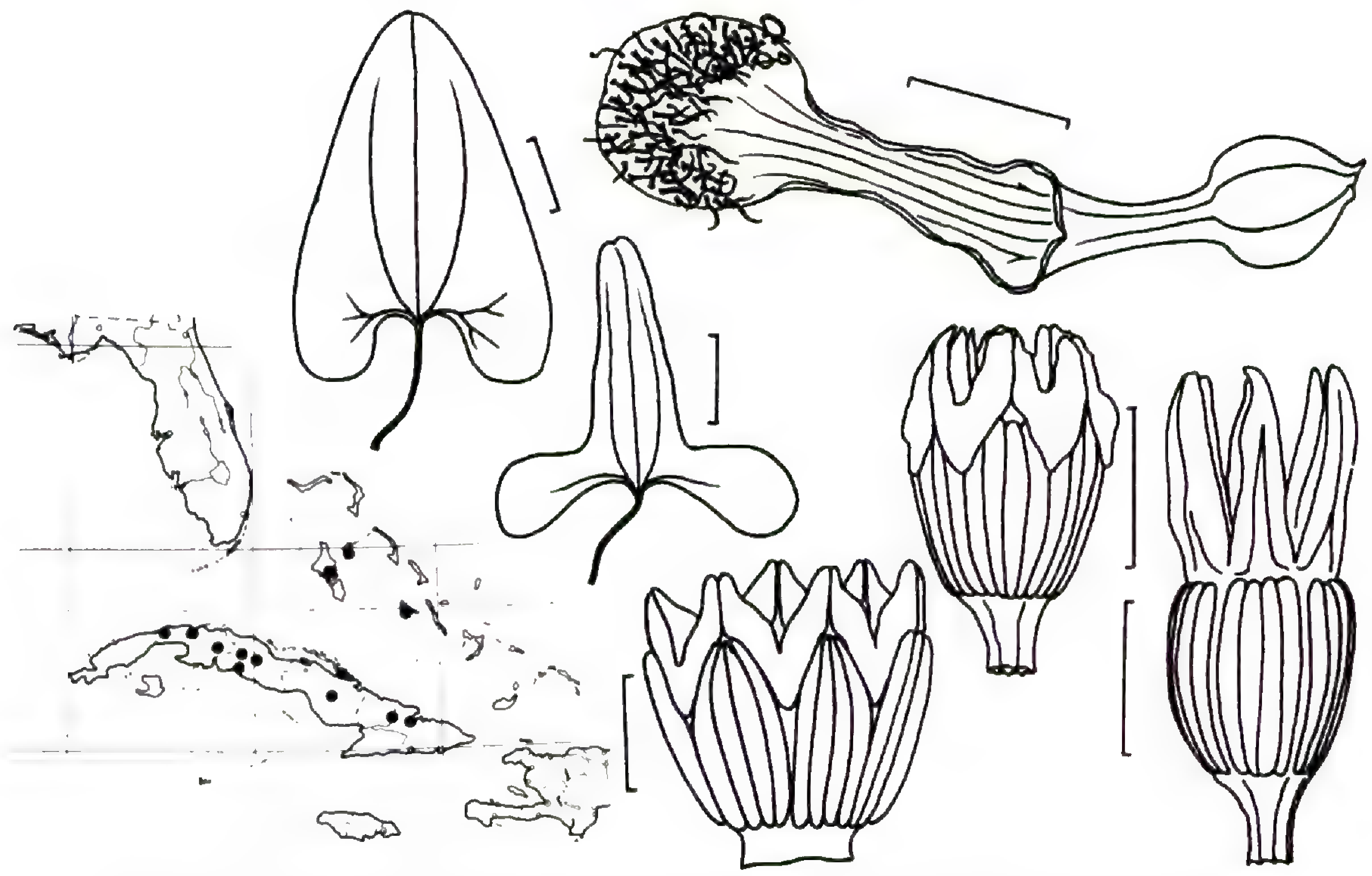


Fig. 30. Distribution, leaves, gynostemia and flower of *A. passifloraefolia.*

septifragally, the hypanthium absent. *Seeds* numerous, flat, 7 mm wide, 8 mm long, 0.5 mm thick.

In dry thickets, Cuba and the Bahamas.

Cuba: Camagüey, Habana, Matanzas, Oriente, Santa Clara.
Bahamas: Andros, Great Exuma, New Providence Islands.

The flowers and leaves of *A. passifloraefolia* are quite variable. The length of the limb varies inversely with the length of the tube; i.e. the tube may split farther, becoming shorter, the limb correspondingly longer. Leaf shapes, even on a single branch, have a range making adequate description impossible.

29. Aristolochia labiata Willd., Mem. Soc. Nat. Mosc. **2:** 101, *t.* 6, 1809. (ex ic.)—Fig. 31.

A. ringens Link & Otto, Abbild. auserl. Gewächse **3:** 33, *t. 13,* 1821, excl. syn. (ex ic.)
A. labiosa Ker-Gawl. in Edwards, Bot. Reg. *t. 689,* 1822. (ex ic.)
A. brasiliensis Mart. & Zucc., Nov. Gen. Sp. Pl. **1:** 77, 1824. (ex ic. cit.)
A. galeata Mart. & Zucc., loc. cit. 76, *t. 50.* (ex ic.)
Ambuya labiosa (Ker-Gawl.) Raf., Fl. Tellur. **4:** 98, 1838.
Aristolochia ornithocephala Hook., Bot. Mag. *t. 4120,* 1844. (ex ic.)
Howardia galeata (Mart. & Zucc.) Klotzsch, Monatsb. Acad. Berlin **1859:** 608, 1859, excl. syn.
Aristolochia brasiliensis Mart. & Zucc. *β macrophylla* Duchr., Man. Gén. Pl. **4:** 30, 1862. (Based on *A. ornithocephala* Hook.)
A. brasiliensis Mart. & Zucc. *γ parviflora* Duchr. in DC., Prod. **15**(1): 471, 1864. (Based on *A. labiata* Willd.)

Stout, glaucous *lianas. Leaves* glabrous, broadly cordate, obtuse at the apex, 7-15 cm broad, 7-12 cm long, green above, beneath gray. *Pseudostipules* large, sessile, amplexicaul, ruffled. *Flowers* solitary in the leaf axils, ebracteolate, geniculate, mottled red, yellow, green and purple, the utricle subglobose, 7 cm long,

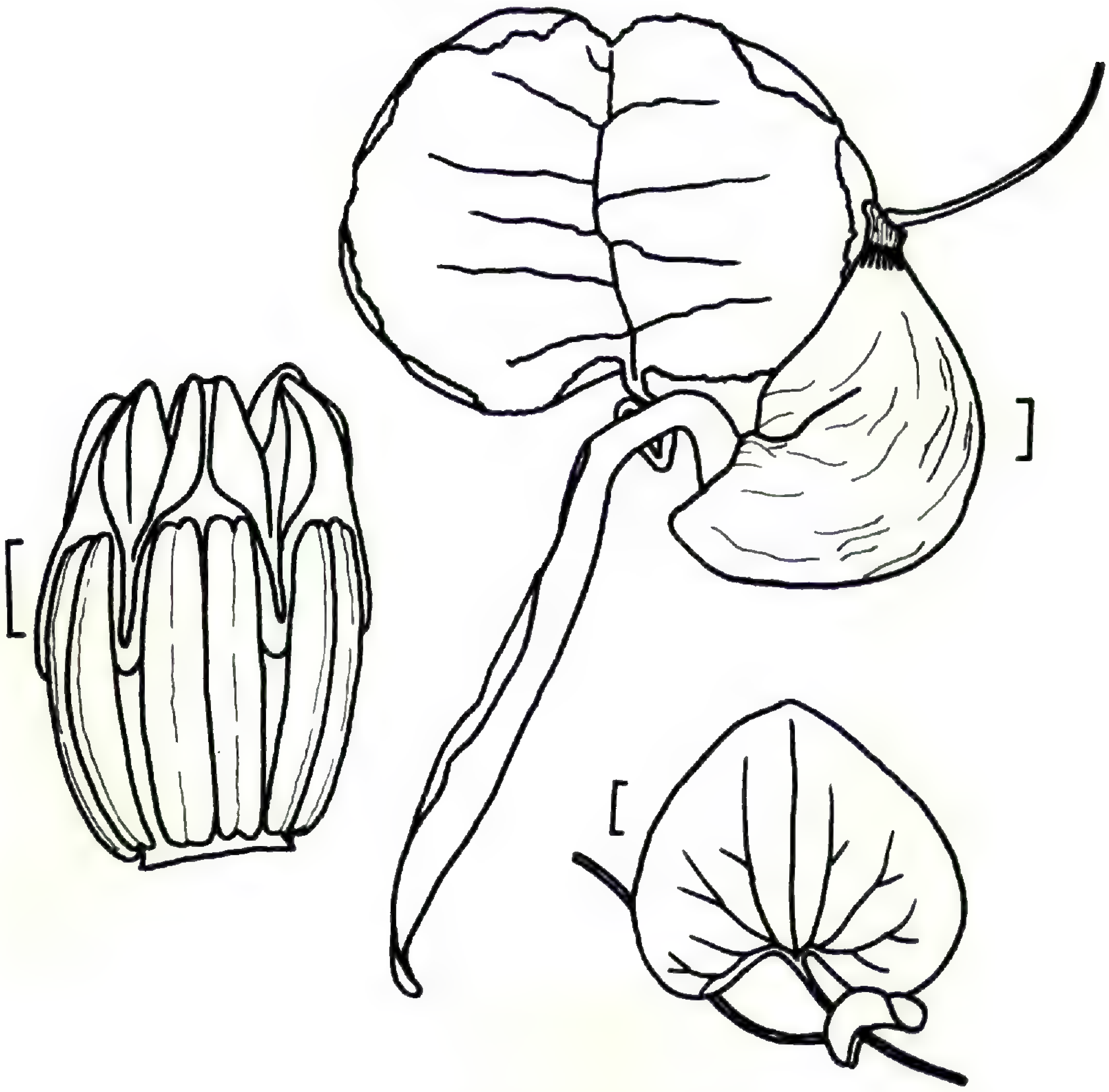


Fig. 31. Gynostemium, flower and leaf showing pseudostipule of *A. labiata*. The flower is drawn with the upper ruffled, orbiculate lobe folded into an erect position; it normally hangs pendent.

syrinx absent, the tube straight, emerging from the side of the utricle at a sharp angle, 4 cm long, annulus absent, the limb with 2 superposed lobes, the upper lobe oblate-orbicular, narrowly clawed, ruffled, deflected and pendent, 14-18 cm wide, 13-15 cm long (including claw), the lower lobe stiffly erect, narrowly lanceolate, 10-15 cm long. *Gynostemium* 6-lobed, the lobes connivent-erect, 1 cm high, 6 mm broad, the anthers 6, equidistant. *Fruits* cylindric, 8 cm long, 3 cm wide. *Seeds* numerous, as in *A. ringens* Vahl.

Aristolochia labiata, a South American plant, in our area is known only from cultivated plants; it may be becoming naturalized in some areas.

A proven hybrid exists between *A. labiata* Willd. and *A. trilobata* L. and was described in the Gardeners' Chronicle (Anon., **50:** 300, 1911.) as *A.* × *kewensis* W. W. It was later again described by Ekman & Schmidt as *A. domingensis* (Notizbl. Bot. Gart. Berlin **12:** 393, 1935).

30. Aristolochia ringens Vahl, Symb. Bot. **3:** 99, 1794. (ex ic. cit.)—Fig. 32.

A. grandiflora Vahl, loc. cit. **2:** 94, *t. 47,* 1791, non Swartz (1788), nec Gomez (1803), nec Arruda (1816). (ex ic.)
Howardia ringens (Vahl) Klotzsch, Monatsb. Acad. Berlin **1859:** 607, 1859.

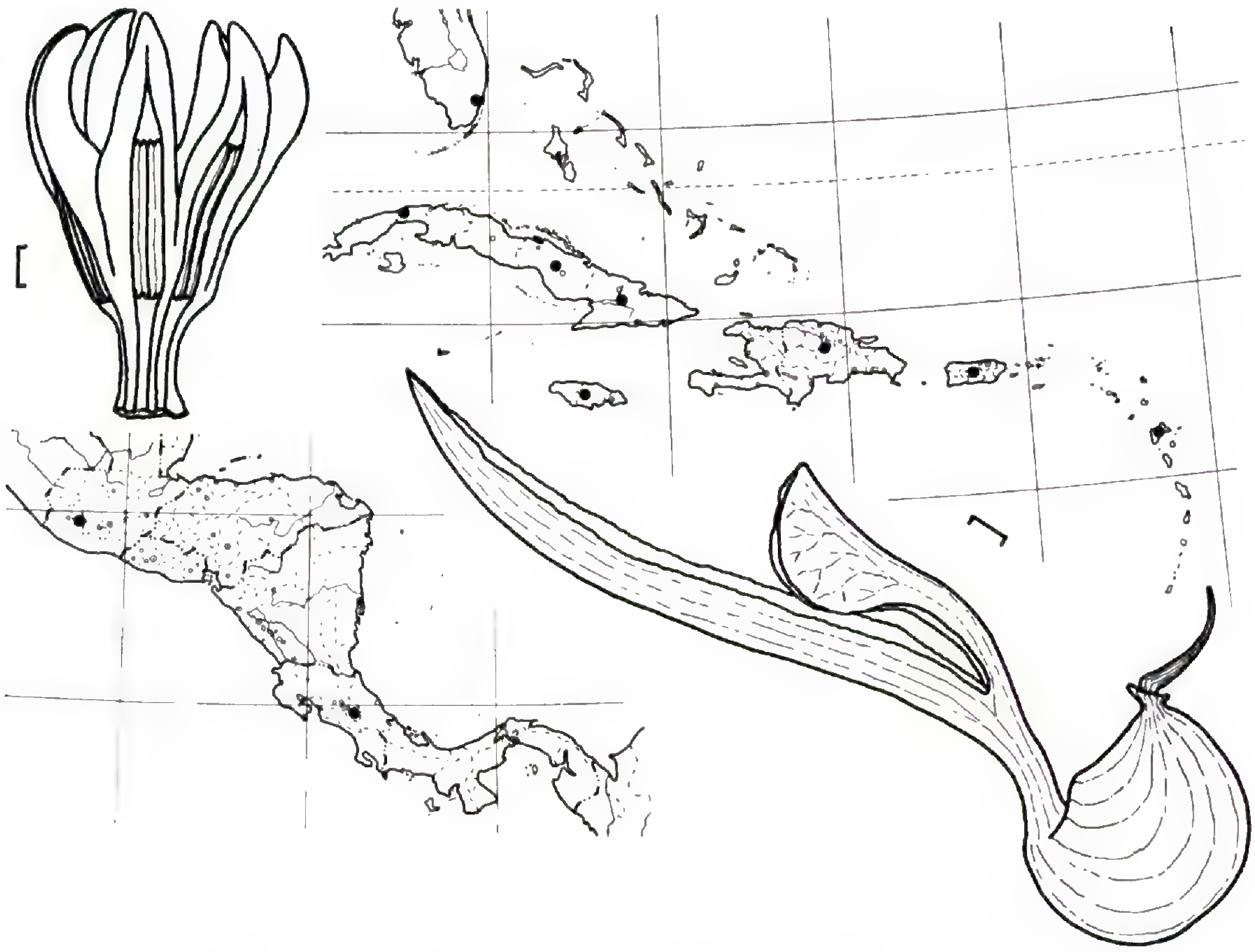


Fig. 32. Gynostemium, distribution and flower of *A. ringens.*

Stout, glaucous *lianas. Leaves* glabrous, broadly cordate, obtuse at the apex, 7-15 cm broad, 7-12 cm long, green above, beneath gray. *Pseudostipules* large, sessile, amplexicaul, ruffled. *Flowers* solitary in the leaf axils, ebracteolate, geniculate, mottled red, yellow, green and purple, the utricle subglobose, 7 cm long, syrinx absent, the tube straight, emerging from the side of the utricle at a sharp angle, 4 cm long, annulus absent, the limb with 2 superposed lobes, the upper lobe obovate-spatulate, not deflected, 4-5 cm wide, 8 cm long, the lower lobe stiffly erect, narrowly lanceolate, 16-20 cm long. *Gynostemium* 6-lobed, the lobes spreading-coroniform, 1 cm high, 8 mm broad, the anthers 2.5-3.0 cm wide, dehiscence acropetal, septifragal, the hypanthium present, bent. *Seeds* numerous, narrowly cordate, flat, 7 mm wide, 12 mm long, 0.2 mm thick.

Aristolochia ringens is naturalized in Florida. I suspect it is a native of South America and only secondarily introduced in our area.

United States. Florida: Dade county.
Guatemala: Guatemala.
Costa Rica: Cartago.
Cuba: Habana, Camagüey, Oriente. Jamaica. Dominican Republic. Puerto Rico. Guadeloupe.

Aristolochia ringens and *A. labiata* probably hydridize to form *A. cymbifera* Mart. & Zucc.

31. Aristolochia **esoterica** Pfeifer, sp. nov.—Fig. 33.

Caules volubiles scandentes. *Folia* firmiter membranacea late cordata apice obtusa 12-16 cm lata 9-12 cm longa supra viridia laevia subtus argenteo-viridia subtiliter tomentulosa, venis fulvo-purpureis. *Pseudostipulae* nullae. *Flores* magni geniculati purpurei; utriculus lacrimiformis 2.5 cm longus, sine syringe; tuba curvata sensim ampliata 3.0 cm longa; limbus 1-lobatus subtriangulatus circa 5 cm latus 6 cm longus, sine appendice. *Columna* 6-loba; stamina 6. *Fructus* ignotus.—Holotypus: *Richard s.n.,* P (Sine loco verisimiliter ex Antillis sinon America Australe.)

Scandent *lianas. Leaves* firmly membranous, broadly cordate, apically obtuse, 12-16 cm broad, 9-12 cm long, smooth, dark-green above, beneath minutely silvery-green, tomentulose, the veins brown-purple. *Pseudostipules* absent. *Flowers* large, geniculate, purplish, the utricle lacrimiform, 2.5 cm long, syrinx absent, the tube bent, gradually opening, 3.0 cm long, the limb 1-lobed, subtriangular, ca 5 cm wide, 6 cm long, unappendaged. *Gynostemium* 6-lobed, the anthers 6. *Fruits* not seen.

The sole specimen yields little information. The leaves are particularly distinct. A similar specimen from Departamento Izabal, Guatemala (*Steyermark 41790,* F), is sterile, making positive identification uncertain.

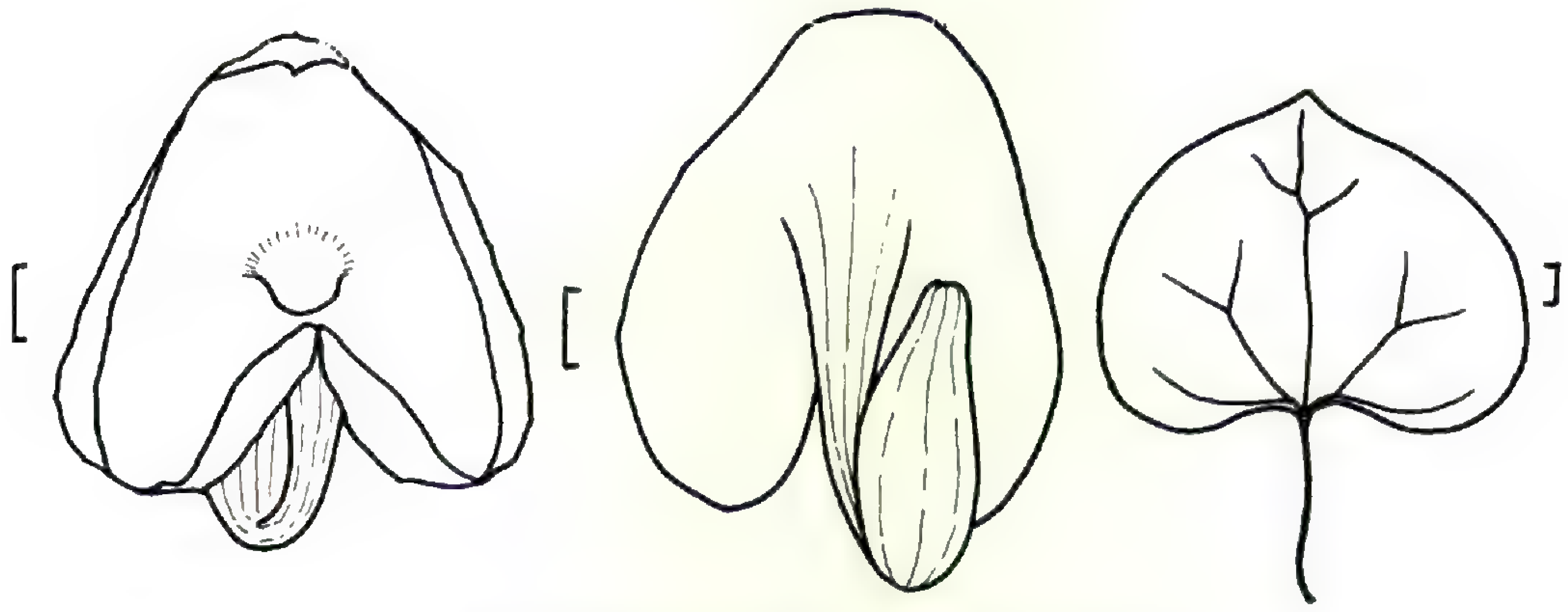


Fig. 33. Flowers and leaf of *A. esoterica.*

32. Aristolochia gigantea Mart. & Zucc., Nov. Gen. Sp. Pl. **1:** 75, *t. 48,* 1824, non Hook. (1846). (ex ic.)—Fig. 34.

Howardia gigantea (Mart. & Zucc.) Klotzsch, Monatsb. Acad. Berlin **1859:** 610, 1859. (quoad syn. Mart.)
Aristolochia clypeata J. Linden & André, Illus. Hort. **17:** *t. 40,* 1870. (ex ic.)
A. sylvicola Standl., Jour. Wash. Acad. Sci. **15:** 5, 1925. (Type: *Standley 27469,* US)

Large, strong-growing *lianas. Leaves* broadly ovate-triangular, acuminate, basally subtruncate, 10-15 cm broad, 12-16 cm long, deep green, glabrous above, beneath white-tomentose. *Pseudostipules* absent. *Flowers* cauliflorous, ebracteolate, geniculate, purple and yellow-orange, the utricle sublacrimiform, gibbous, 10 cm long, syrinx absent, the tube not sharply differentiated from the utricle and limb, U-shaped, ca 4 cm long, annulus absent, the limb 1-lobed, abruptly spreading

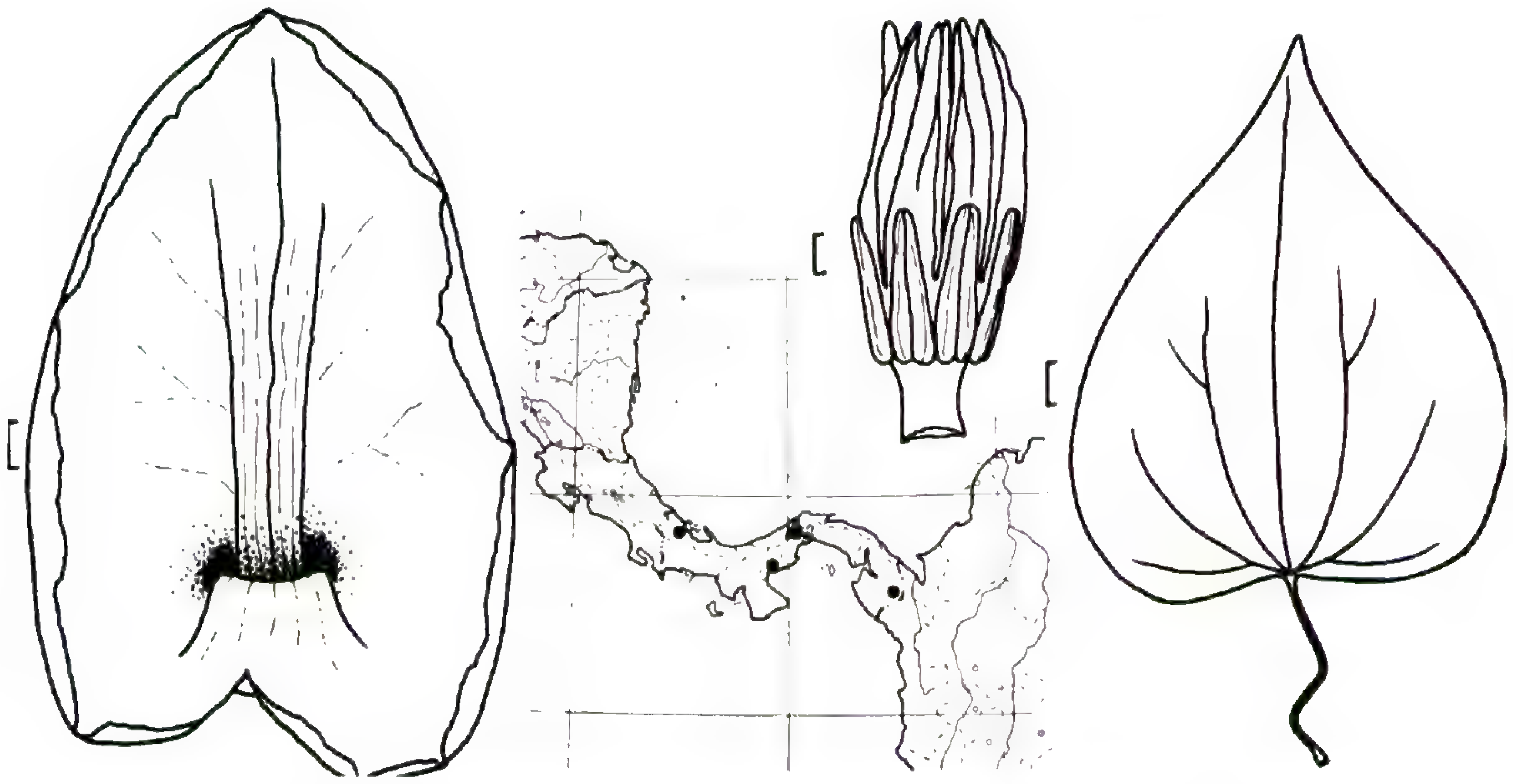


Fig. 34. Face view of flower, distribution, gynostemium and leaf of *A. gigantea.*

from the tube, broadly cordate, ca 14 cm wide, 16 cm long, unappendaged. *Gynostemium* 6-lobed, 1 cm high, 4 cm broad, the anthers 6, equidistant. *Fruits* large, glaucous, 8 cm long, 2.5-3.0 cm wide, dehiscence acropetal, septifragal, the hypanthium curved, 5 mm long. *Seeds* numerous, flat, 5 mm wide, 7 mm long, very thin, papery.

Wet rain forests, Panama.

Panama: Bocas del Toro, Canal Zone, Coclé, Darien.

Of South American affinities, *A. gigantea* is distinct in its flower and leaf shape from all other species in our area.

33. Aristolochia littoralis Parodi, Anal. Soc. Cient. Argent. **5:** 155 (Contrib. 47), 1878. (Type: *Parodi s.n.*, not seen)—Fig. 35.

A. elegans Mast., Gard. Chron., n.s., **34:** 301, *t. 61,* 1885. (Type: *Glaziou 13163,* not seen)
A. hassleriana Chod., Bull. Herb. Boiss. **7:** App. 1, 61, 1899. (Type: *Hassler 3365,* not seen)
A. elegans Mast. var. *hassleriana* (Chod.) Hassl. in Fedde, Repert. Sp. Nov. **11:** 177, 1912.

Vigorous, glacous *lianas. Leaves* cordate-reniform, obtuse at the apex, basally cordate, 6-10 cm broad, 7-9 cm long, smooth, green above, beneath gray-green, heavily glaucous. *Pseudostipules* auriculate, amplexicaul, pale green. *Flowers* solitary in the leaf axils, ebracteolate, geniculate, greenish-yellow and deep black-purple, the utricle subcylindric, 3.5 cm long, syrinx absent, the tube bent, 3 cm long, annulus absent, the limb 1-lobed orbiculate, abruptly spreading from the tube, 10 cm wide, 10 cm long. *Gynostemium* 6-lobed, 8 mm high, 5 mm broad, the anthers 6, equidistant. *Fruits* cylindric, 4.5 cm long, 2.5 cm wide, dehiscence acropetal, septifragal, the hypanthium retilinear from the ovary. *Seeds* numerous, flat, 4 mm wide, 6 mm long, 0.5 mm thick.

Commonly growing in second growth forests as an escape from wide cultiva-

Fig. 35. Distribution, flowers and gynostemium of *A. littoralis.*

tion, its native area obscure, but probably South American; in our region ubiquitous in cultivation in the tropic areas.

UNITED STATES. FLORIDA: Hillsborough county.
MEXICO: Mexico, Nuevo León.
GUATEMALA: La Libertad.
NICARAGUA: Managua.
BERMUDA. CUBA: Habana, Sta. Clara. JAMAICA. HAITI. DOMINICAN REPUBLIC. ST. KITTS. BARBUDA. GUADELOUPE.

34. ARISTOLOCHIA ODORATISSIMA L., Sp. Pl. 1362, 1763, non Vell. (1827), nec Benth. (1841). (ex char.)—Fig. 36.

A. 1 scandens P. Browne, Civ. & nat. hist. Jamaica 329, 1756. (ex char.)
A. pandurata Jacq., Hort. Schoenbr. **4**: 49, *t. 497,* 1804, non Wall. ex Duchr. (1864). (ex ic. cit.)
A. panduriformis Willd., Sp. Pl. **4**: 152, 1805. (Based on *A. pandurata* Jacq.)
A. picta Karst., Auswahl neuer und schönbluhender Gewächse Venezuelas 24, *t. 8,* 1848, pro. syn.
Howardia pandurata (Jacq.) Klotzsch, Monatsb. Acad. Berlin **1859**: 619, 1859.
Aristolochia aurantiaca Duchr. in DC., Prod. **15**(1):475, 1864. (Type: *Linden 310,* photo G-DC)
A. moschata Wedd. ex Duchr., loc. cit., pro syn.
A. odoratissima L. *β grandiflora* Duchr., loc. cit. (Type *Linden 49,* photo G-DC)
A. ottonis Klotzsch ex Duchr., loc. cit. 476, pro syn.
Howardia warscewiczii Klotzsch ex Duchr., loc. cit. pro syn. (Type: *Warscewicz s.n.,* not seen)

Fig. 36. Flower, leaf, gynostemium and distribution of *A. odoratissima.*

Aristolochia pandurata Jacq. *β warscewiczii* (Klotzch ex Duchr.) Duchr., loc. cit (ex char.)
A. rimbachii Schmidt in Fedde, Repert. Sp. Nov. **23**: 287, 1927. (Type: *Rimbach* 37, photo MO)
A. martiniana Standl., Field Mus. Pub. Bot. **17**: 238, 1937. (Type: *Klug 4168*, F, MO, NY, US)
A. odoratissima L. var. *pandurata* (Jacq.) Hoehne, Fl. Brasílica **15** (2): 47, 1942.

Glabrous *lianas. Leaves* membranous, cordate-subpandurate to triangular, medially constricted, acuminate, basally cordate-hastate, 5-9 cm broad, 8-12 cm long, glabrous. *Pseudostipules* absent. *Flowers* solitary in the leaf axils, ebracteolate, geniculate, purple and yellow, the utricle lacrimiform, gibbous, 3 cm long, syrinx absent, the tube bent at its origin on side of utricle, 2-3 cm long, annulus absent, the limb 1-lobed, abruptly spreading from the tube, 4-6 cm wide, 10-13 cm long, tapering to an acuminate apex at the upper medial border. *Gynostemium* 6-lobed, 4-5 mm high, 2-3 mm broad, the anthers 6, equidistant. *Fruits* cylindric, ribbed, arcuate, 7-10 cm long, 1 cm wide, dehiscence acropetal, septifragal, the hypanthium sharply deflected and bent, 7 mm long. *Seeds* numerous, subrevolute, 2 mm wide, 3 mm long, 1 mm thick.

In hot, wet secondary growth and forested areas, Mexico to Panama, and sparsely in the West Indies.

Mexico: Michoacán, Tabasco.
Guatemala: Petén.
Honduras: Atlántida, Cortés.
Costa Rica: Limón, Nicoya.
Panama: Bocas del Toro.
Jamaica. St. Thomas. Martinique.

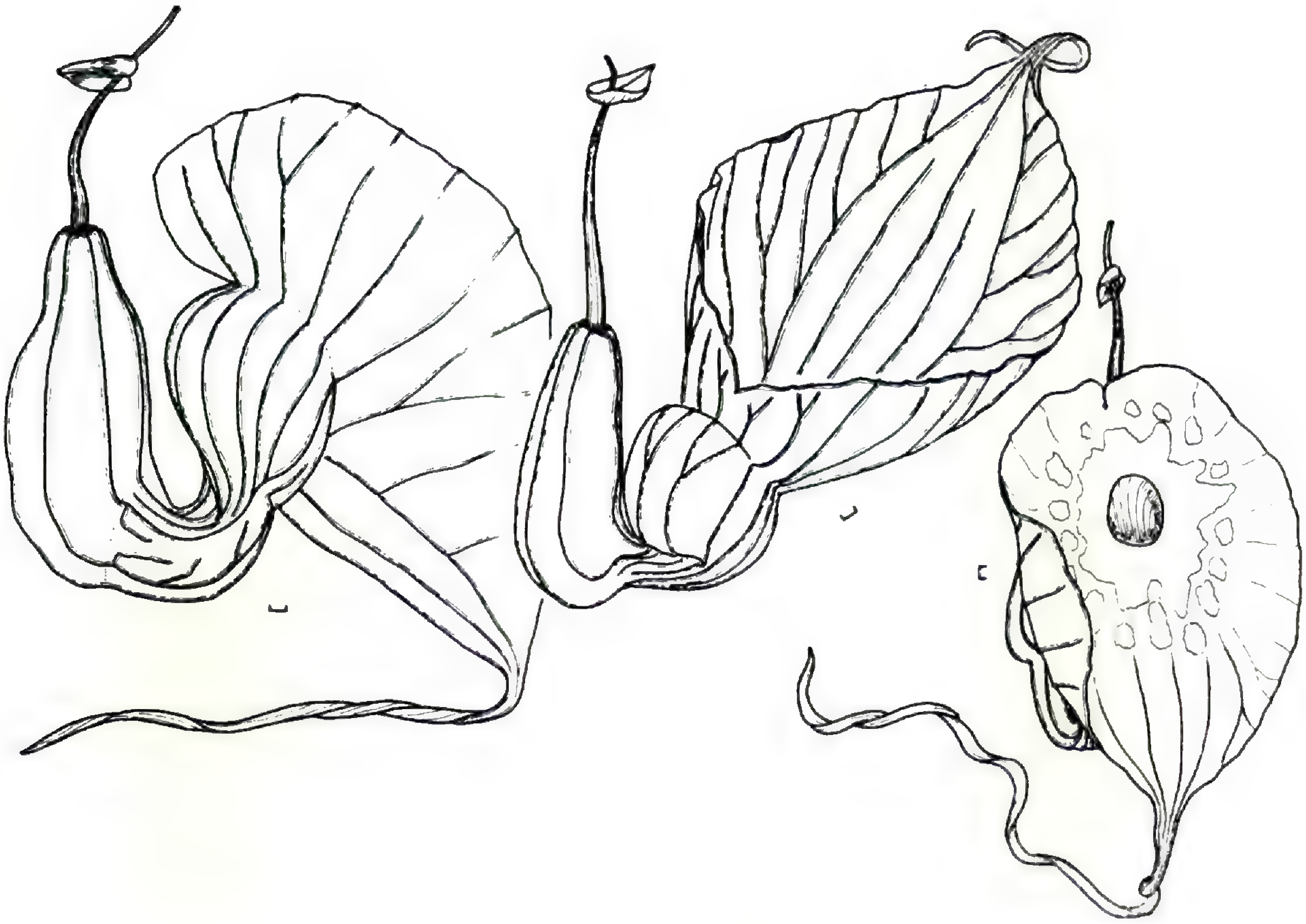


Fig. 37. Flower and distribution of *A. grandiflora*.

35. ARISTOLOCHIA GRANDIFLORA Sw., Prod. Veg. Ind. Occ. 126, 1788, non Vahl (1791), nec Gomez (1803), nec Arruda (1816). (Type: *Swartz s.n.*, S)—Fig. 37.

A. 2 scandens P. Browne, Civ. & nat. hist. Jamaica 329, 1756, non Mill. (1768). (ex char.)
A. cordiflora Mutis ex H.B.K., Nov. Gen. Sp. Pl. **2:** 149, 1817. (Type: *Mutis s.n.*, not seen)
A. foetens Lindley, Bot. Reg. *t. 1824*, 1836. (ex ic.)
A. gigas Lindley, loc. cit. *t. 60*, 1842. (Type: *Hartweg s.n.*, not seen)
A. gigantea Hook., Bot. Mag. *t. 4221*, 1846. (ex ic.)
Howardia gigantea (Hook.) Klotzsch, Monatsb. Acad. Berlin **1859:** 610, 1859. (quoad syn. Hook.)
H. grandiflora (Sw.) Klotzsch, loc. cit.
Aristolochia grandiflora (Sw.) *β hookeri* Duchr. in DC., Prod. **15**(1):473, 1864. (Based on *A. gigantea* Hook.)

Strong-growing, glabrescent *lianas. Leaves* triangular-cordate, apex acute to acuminate, basally deeply cordate, 8-15 cm broad, 10-20 cm long, deep green, smooth above, beneath strigose in juvenile leaves, becoming smooth with age, paler. *Pseudostipules* absent. *Flowers* solitary in leaf axils, bracteolate, more or less twice-geniculate (once at the tube flexure and again at the annulus), variously blotched with purple, white, yellow, red and green, very variable in size over a vast range, but commonly very large, the utricle lacrimiform, gibbous, 6-18 cm long, syrinx cylindric, as long as 4 cm, directed obliquely into the utricle, the tube bent at its middle, 7-15 cm long, annulus thin, sharp-edged, the limb abruptly spreading from the annulus and tube, 1-lobed, 20-50 cm or more wide, 0.5-3.0 m long, including the length of the pendent, tape-like appendage on the lower border of the limb. *Gynostemium* 6-lobed, coroniform, 1.5 cm high, 1.0 cm broad, the anthers 6, equidistant. *Fruits* cylindric, 10 cm long, 4 cm wide, dehiscence acropetal, septifragal, hypanthium absent. *Seeds* numerous, triangular, flat, 1 cm wide, 1.2 cm long, 2 mm thick.

Common along streams and in secondary-growth thickets from tropical Mexico to Panama and the West Indies.

MEXICO: Chiapas, Oaxaca, Vera Cruz, Yucatán.
GUATEMALA: Alta Verapaz, Chiquimula, El Progreso, Escuintla, Guatemala, Izabal, Jalapa, Retalhuleu, San Marcos, Santa Rosa, Zacapa.
BRITISH HONDURAS: Caya, Kendall, Stann Creek.
EL SALVADOR: San Salvador, Morazán.
HONDURAS: Atlántida, Cortés, Santa Barbara.
NICARAGUA: Granada.
COSTA RICA: Limón, San José, Talamanca.
PANAMA: Darien, Nombre de Díos.
CUBA: Las Villas. JAMAICA. ST. THOMAS. MARTINIQUE. TRINIDAD.

It is possible that more than one species is represented in this taxon, but without further collections and field work to yield an understanding of the variability of the group, this is probably the best disposition.

36. ARISTOLOCHIA EKMANII Schmidt, Arkiv Bot. Stockh. **21A**(5): 1, 1927. (Type: *Ekman H4964*, S, US)—Fig. 38.

Glabrous, subglaucous, twiggy *lianas. Leaves* small, oblong, with 5 basal veins, shallowly cordate, 5-10 mm broad, 1-2 cm long, deep green, with hamate

Fig. 38. Flowers, distribution, gynostemium and leaf of a *A. ekmanii.*

hairs above, beneath smooth, glaucous. *Pseudostipules* absent. *Flowers* solitary in the leaf axils, ebracteolate, extremely arcuate, green, brown, yellow and purple, the utricle ovoid, 5 mm long, syrinx an ineqilateral flap, the tube slightly arched, 5 mm long, the limb 1-lobed, cordate-acuminate, leathery, gradually expanding from the tube, 2 cm wide, 3-4 cm long. *Gynostemium* 6-lobed, 2.5 mm high, 2 mm broad, the anthers 6, equidistant. *Fruits* subspheric-cylindric, 1.5-2.0 cm long, 1.5 cm wide, dehiscence acropetal, septifragal, the hypanthium straight, 5 mm long. *Seeds* numerous, flat, 3 mm wide, 3 mm long, very thin, papery.

In limestone soils, on rocks and shrubs, northern Haiti.

HAITI.

Aristolochia ekmanii is often mistaken for the Cuban *A. tigrina,* but it differs in details of leaf venation, as well as in floral morphology.

37. ARISTOLOCHIA TIGRINA A. Rich., Fl. Cub. Fanerog. **2:** 194, 1850. (Type: *Sagra s.n.,* P)—Fig. 39.

A. elliptica Duchr., Ann. Sci. Nat., sér. 4, **2:** 51, 1854. (Type: *Galeotti 209,* P)

Glabrous, twiggy *lianas. Leaves* small, oblong to obovate with 3 basal veins, obtuse at the apex, basally obtuse to truncate, 5-8 mm broad, 1-3 cm long, smooth. *Pseudostipules* absent. *Flowers* solitary in the leaf axils, ebracteolate, slightly arcuate, green, yellow, spotted purple, the utricle ovoid, gibbous, 7 mm long, syrinx ineqilateral, cylindric, the tube straight, 1 cm long, the limb 1-lobel, triangular, gradually expanding from the tube, ca 1 cm wide, 1.5-2.0 cm long, unappendaged. *Gynostemium* 6-lobel, obconic, 3 mm high, 2.5 mm broad, the anthers 6, equidistant. *Fruits* subspheric, 1.5 cm diameter, dehiscence acropetal, septifragal, the hypanthium straight, 2 mm long. *Seeds* numerous, flat, triangular, 5 mm wide, 5 mm long, 0.2 mm thick.

In rocks, dry soils, Cuba.

CUBA: Habana, Oriente, Pinar del Río, Santa Clara.

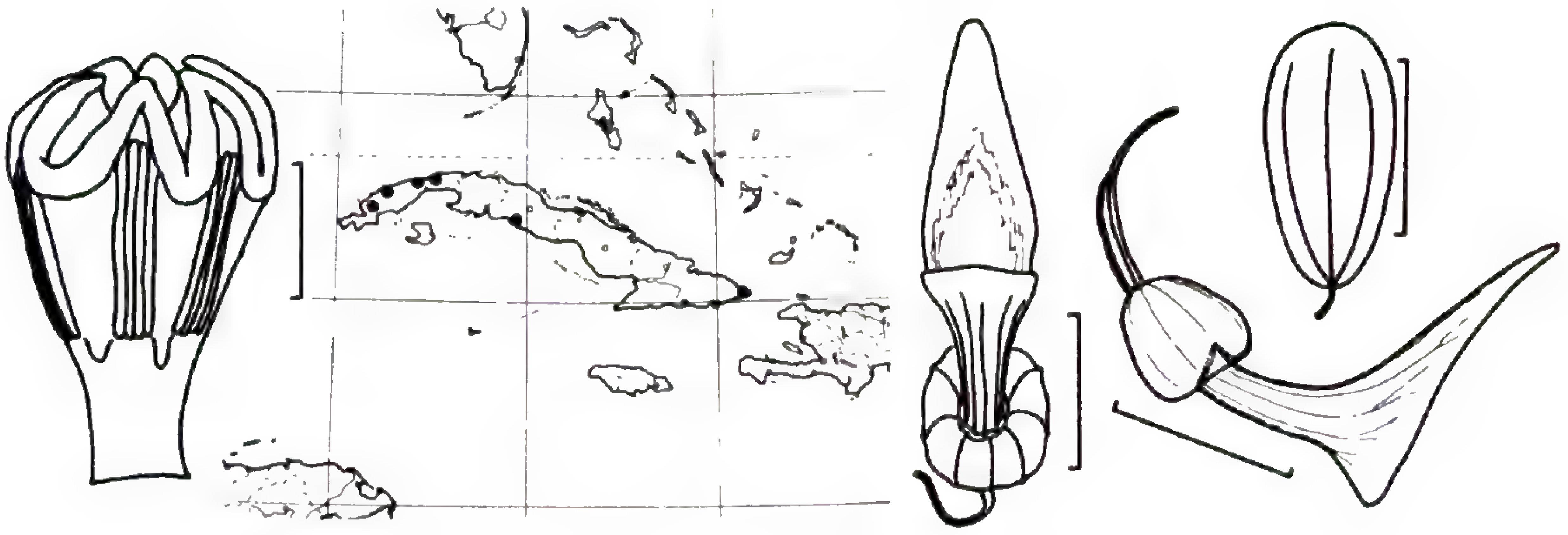


Fig. 39. Gynostemium, distribution, flowers and leaf of *A. tigrina*.

38. Aristolochia samanensis Schmidt, Notizbl. Bot. Gart. Berlin **12:** 393, 1935. (Type: *Ekman H15468*, S)—Fig. 40.

Small, glabrous, glaucous *lianas*. *Leaves* ovate, rounded to obtuse at the apex, basally subtruncate, 2.5 cm broad, 4.5 cm long, deep green and smooth above, beneath prominently glaucous, smooth. *Pseudostipules* absent. *Flowers* solitary in the leaf axils, ebracteolate, leathery, subgeniculate, green, brown and white, the utricle obconic, 8 mm long, syrinx ineqilateral, tubular, the tube short, 7 mm long, the limb 1-lobed, arching sharply upward, smooth, ovate, 1.5 cm wide, 2 cm long, unappendaged. *Gynostemium* broadly 6-lobed, 3 mm high, 4 mm broad, the anthers 6, equidistant. *Fruits* cylindric, glaucous, 3 cm long, 1.75 cm wide, dehiscence acropetal, septifragal, the hypanthium straight, 2 mm long. *Seeds* numerous, flat, triangular, 6 mm wide, 7 mm long, 0.2 mm thick.

Precise locality unknown. Known only from the type specimen.

Dominican Republic.

39. Aristolochia maxima Jacq., Enum. Syst. Pl. 30, 1762; Stirp. Amer. Hist. 233, *t. 146*, 1763, non Cham. (1832). (ex ic.)—Fig. 41.

A. geminiflora H.B.K., Nov. Gen. Sp. Pl. **2:** 148, *t. 117*, 1817. (ex ic.)
A. mexicana Dietr., Syn. Pl. **5:** 196, 1852 (fide Duchr., 1864), non Willd. (1805), nec Kostel. (1831).
Howardia geminiflora (H.B.K.) Klotzsch, Monatsb. Acad. Berlin **1859:** 619, 1859.
H. gollmerii Klotzsch, loc. cit. 621. (Type: *Gollmer s.n.*, not seen)
H. hoffmannii Klotzsch, loc. cit. (Type: *Hoffmann 49*, not seen)
H. maxima (Jacq.) Klotzsch, loc. cit. 615.
Aristolochia biflora Willd. ex Duchr. in DC., Prod. **15**(1): 457, 1864. (Based on *A. geminiflora* H.B.K.)
A. maxima L. (1763) *α maxima* Duchr., loc. cit. 456.
A. maxima L. *β geminiflora* (H.B.K.) Duchr., loc. cit. 457.
A. maxima L. *γ augustifolia* Duchr., loc cit., (Type: *Hoffman 49*, not seen.)
A. reticulata Holton ex Duchr., loc. cit., non Nutt. (1835). (ex char.)
A. oblongifolia Brandg., Univ. Calif. Pub. Bot. **10:** 404, 1924. (Type: *Purpus 9076*, UC)

Sprawling subglabrous *lianas*. *Leaves* oblong to spatulate, obtuse to apiculate at the apex, basally truncate to shallowly subcordate, 3-7 cm broad, 6-12 cm long, glabrous or glabrescent, beneath with prominent, raised reticulate venation.

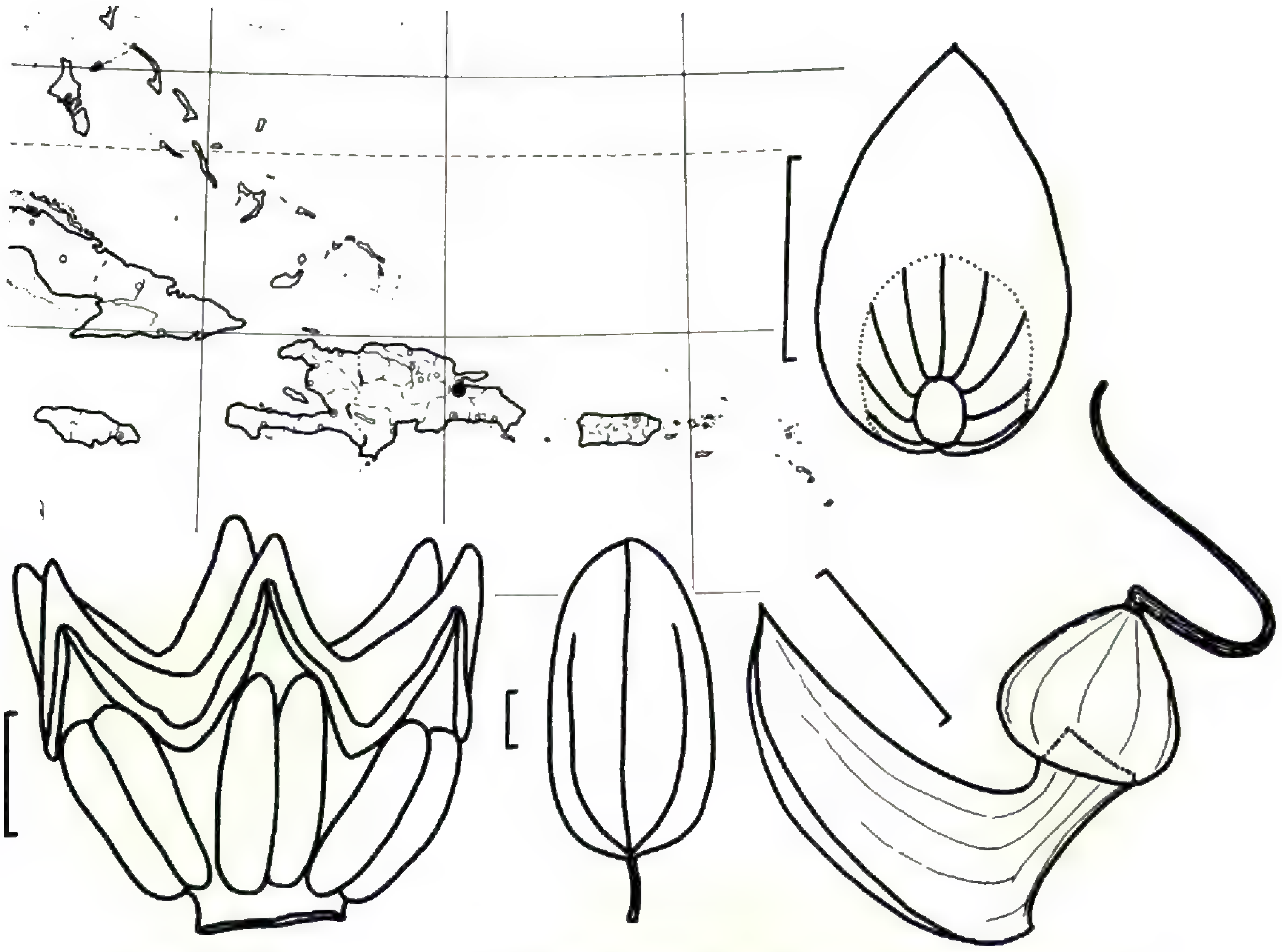


Fig. 40. Gynostemium, leaf, distribution and flowers of *A. samanensis*.

Pseudostipules absent. *Flowers* in several-branched axillary, racemose clusters, bracteolate, geniculate, purple, the utricle ovoid, 2.5 cm long, syrinx absent, the tube bent, 2 cm long, the limb 1-lobed, ovate, gradually expanding from the tube, 3-4 cm wide, 5-6 cm long. *Gynostemium* 6-lobed, 5 mm high, 4 mm broad, the anthers 6, equidistant. *Fruits* very large, pendent, 10-15 cm long, 7-10 cm wide, dehiscence acropetal, septifragal, exposing latticed septa, the hypanthium absent. *Seeds* very numerous, flat, triangular, 15 mm wide, 10 mm long, 1 mm thick.

Along streams and in moist thickets, in southern Florida, southern Mexico southward throughout Central America; common.

United States. florida: Dade county.
Mexico: Chiapas, Campeche, Yucatán.
Guatemala: Alta Verapaz, Chiquimula, Escuintla, Guatemala, Jutiapa, Retalhuleu, Santa Rosa, Zacapa.
British Honduras: Belice.
El Salvador: Ahuachapán, La Unión, San Salvador.
Honduras: Atlántida, Comayagua, Morazán.
Costa Rica: San José.
Panama: Panama.
Martinique.

This is the commonest *Aristolochia* species in Central America. It is confused with all of the Central American species with oblong leaves, but needlessly so, since the others all have leaves which are tomentose beneath while *A. maxima* is essentially smooth and devoid of hairs when mature. The subspatulate outline of its leaves is a further aid to identification.

Fig. 41. Gynostemium, distribution, flower and leaf of *A. maxima*.

40. Aristolochia **chasmema** Pfeifer, sp. nov.—Fig. 42.

Caules glabri volubiles laeves. *Folia* angustio triangulata vel oblongata apice rotundata basi truncata 11-16 mm lata 4-5 cm longa supra viridia laevia subtus glauca laevia. *Pseudostipulae* nullae. *Flores* axillares solitarii ebracteolati arcuati virides flavi fulvi; utriculus ovoideus 8 mm longus; syrinx tenuis inaequilateralis tubiformis brevis; tuba tenuis arcuata 20 mm longa; limbus 2-lobus labro supero longissimo lanceolato subacuto erecto 3.8 cm longo labro infero brevi rotundato nonnihil erecto 0.8 cm longo. *Columna* 6-loba obconica brevis stipitata 2.5-3.0 mm alta 2 mm lata; stamina 6 ad libram aequilateralia. *Capsula* subcylindriformis 2 cm longa 12 mm lata basi dehiscens; hypanthium absens; semina ignota. —Holotypus: *Ekman H6740,* US ("Hispaniola. Civ. *Haiti*: Massif de la Pelle, gr. Morne des Commissaires, Anses-á-Pitre, road to Banane, at Riv. Pedernales, c. 150 m., not rare. 25. VIII. 1926."). Isotypi: MO, S.

Glabrous smooth *lianas*. *Leaves* narrow triangulate to oblong, apex rounded, base truncate, 11-16 mm wide, 4-5 cm long, green and smooth above, beneath glaucous and smooth. *Pseudostipules* absent. *Flowers* solitary in the leaf axils, ebracteolate, arcuate, green, yellow and brown, the utricle ovoid, 8 mm long, syrinx a thin unequally short tube, the tube narrow, arcuate, 20 mm long, the limb 2-lobed, the upper lobe very long, lanceolate, subacute, erect, 3.8 cm long, the lower lobe short, rounded, somewhat erect, 0.8 cm long. *Gynostemium* 6-lobed obconic, short-stipitate, 2.5-3.0 mm high, 2 mm broad, the anthers 6, equidistant. *Capsule*

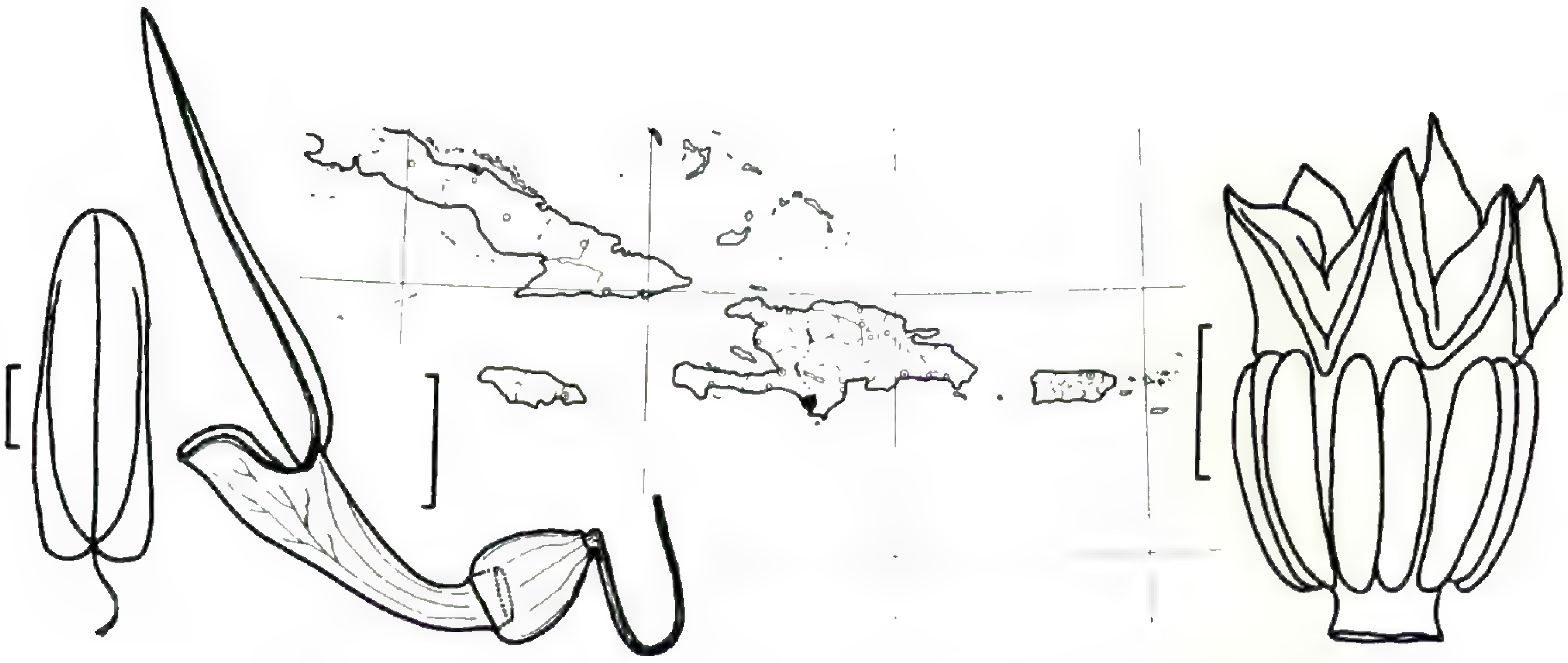


Fig. 42. Leaf, flower, distribution and gynostemium of *A. chasmema.*

subcylindric, 2 cm long, 12 mm wide, dehiscence acropetal, the hypanthium absent. *Seeds* not seen.

Known only from the type collection.

HAITI.

The glaucous, smooth leaves of *A. chasmema* may be mistaken for *A. samanensis,* but their flowers are extremely distinctive.

41. ARISTOLOCHIA OVALIFOLIA Duchr., Ann. Sci. Nat., sér. 4, **2:** 50, 1854. (Type: *Galeotti 213,* P)—Fig. 43.

Guaco mexicana Liebm., Forhandl. Skandin. Naturf. **1844:** 203, 1847, non *Aristolochia mexicana* Willd. (1805), nec Kostel. (1831), nec Dietr. (1839). Type: *Liebmann 409,* US; photos, F, GH, MO)

Puberulent *lianas. Leaves* elliptic-ovate, apiculate, shallowly cordate, 3-6 cm broad, 5-12 cm long, smooth above, beneath finely puberulent, particularly on the raised reticulum of veins. *Pseudostipules* absent. *Inflorescence* short, 2- to 8-flowered, racemose, axillary. *Flowers* bracteolate, arcuate, brown with yellow throat, the utricle subpyriform, 1.5 cm long, syrinx cylindric, 3 mm high, the tube arcuate, 2.5 cm long, the limb 1-lobed, gradually expanding from the tube, in mature flowers sharply revolute along the lateral margins, 1.75 cm wide, 5 cm long, unappendaged. *Gynostemium* fusiform, 5-6 mm high, 3 mm broad, the anthers 6, equidistant. *Fruits* ovoid, large, 8-10 cm long, 4-5 cm wide, dehiscence acropetal, septifragal, the hypanthium absent. *Seeds* numerous, flat, cordate, 8 mm wide, 7 mm long, 0.5 mm thick.

Found in wet, secondary forest growth, in extreme southern Mexico and British Honduras, chiefly in the eastern drainage area.

MEXICO: Oaxaca, Tabasco.
BRITISH HONDURAS: Middlesex.

Fig. 43. Leaf, distribution, gynostemium, flower and immature flower bud of *A. ovalifolia.* Note that the configuration of young buds bear little resemblance to the mature flower.

This species is easily confused with *A. maxima,* but differs in leaf shape, floral conformation and seeds. *Aristolochia ovalifolia* is mentioned on the labels of 3 sheets of *Schipp 384,* from the Gray Herbarium, University of California Herbarium and the Missouri Botanical Garden Herbarium as being "common," "occasional" and "rare," respectively.

42. Aristolochia linearifolia Griseb., Cat. Pl. Cub. 115, 1866. (Type: *Wright 2617,* MO, NY, S)—Fig. 44.

A. stenophylla Urban, Symb. Antill. **3**: 281, 1902. (Type: *Jicarda 1281,* NY)

Glabrous *lianas. Leaves* linear to narrowly triangular, acute at the apex, basally acute to truncate or very shallowly cordate, 4-16 mm broad, 5.5 to 11 cm long, smooth above, beneath with emersed, reticulate venation. *Pseudostipules* amplexicaul, auriculate or absent. *Flowers* solitary in the leaf axils, ebracteolate, geniculate, pale, greenish-yellow with purple stripes, the utricle ellipsoid, 1 cm long, syrinx absent, the tube bent, 2-3 cm long, the limb 1-lobed, narrowly triangular, gradually expanding thence narrowing from the tube, ca 5 mm wide, 1.5-2.5 cm long, unappendaged. *Gynostemium* 6-lobed, 2 mm high, 3 mm broad, the anthers 6, equidistant, convergent at their apices, divergent below. *Fruits* subspheric, 1.5 cm diameter, dehiscence acropetal, septifragal, the hypanthium absent. *Seeds* numerous, flat, 3 mm wide, 3 mm long, 0.2 mm thick.

In thickets, dry soils; Cuba and southern Haiti.

Cuba: Oriente.
Haiti (incl. Gonave I.).

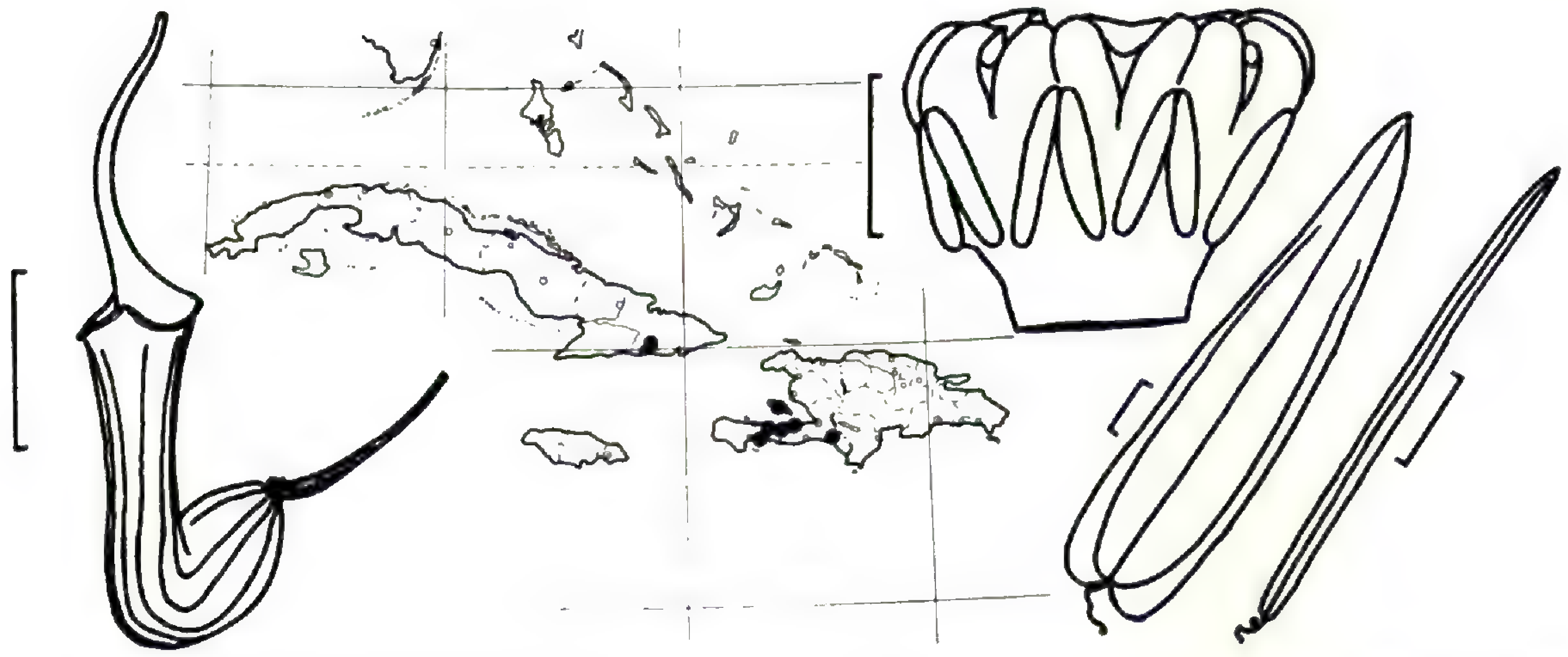


Fig. 44. Flower, distribution, gynostemium and leaves of *A. linearifolia*. The narrow-leaved form is Cuban, the broader-leaved form, Haitian.

The linear-leaved representatives are from Cuba, the triangular-leaved ones from Hispaniola. It may seem reasonable to some to give them subspecific status, but there are too few collections to satisfy me in this regard.

43. Aristolochia bilabiata L., Sp. Pl. 1361, 1763. (ex char., ex ic. cit.)—Fig. 45.

A. oblongata Jacq., Hort. Schoenb. **2:** 29, 1797. (ex char.)
Diglosselis trinervis Raf., Fl. Tellur. **4:** 98, 1838. (Based on *A. bilabiata* L.)
Howardia bilabiata (L.) Klotzsch, Monatsb. Acad. Berlin **1859:** 611, 1859.
Aristolochia conduplicata Poit. ex Duchr. in DC., Prod. **15**(1): 460, 1864. (Type: *Poiteau s.n.*, P)
A. calceiformis Urban, Symb. Antill. **1:** 300, 1899. (Type: *Sintenis 2490,* F, P, S, US)

Puberulent to glabrescent *lianas*. *Leaves* oblong to subtriangular, obtuse to apiculate at the apex, basally shallowly cordate to subtruncate, 2.0-3.5 cm broad, 4.5-6.5 cm long, beneath venation raised-reticulate. *Pseudostipules* large, amplexicaul, orbiculate. *Flowers* on short axillary shoots in axils of reduced leaves, ebracteolate, rectilinear, purple and yellow, the utricle elliptic, 7 mm long, syrinx an inequilateral flange, the tube straight, trumpet-shaped, 2-3 cm long, the limb 1-lobed, gradually expanding from the tube, lanceolate, plicate after anthesis, 7 mm wide, 1 cm long, unappendaged. *Gynostemium* 6-lobed, 2.5 mm high, 2 mm broad, the anthers 6, equidistant. *Fruits* ovoid-cylindric, 2-2.5 cm long, 1.5-1.75 cm wide, dehiscence acropetal, septifragal, the hypanthium absent. *Seeds* numerous, flat, triangular, 4 mm wide, 5 mm long, 0.2 mm thick.

Dry thickets and brush in limestone soils, throughout the Greater Antilles.

Cuba: Camagüey, Habana, Isla de Pinos, Matanzas, Oriente, Pinar del Río. Haiti (incl. Tortue I.). Dominican Republic. Puerto Rico. St. Thomas.

This species seems related to *A. anguicida,* though differs by its narrower leaves and the more shallow lobing of its gynostemium.

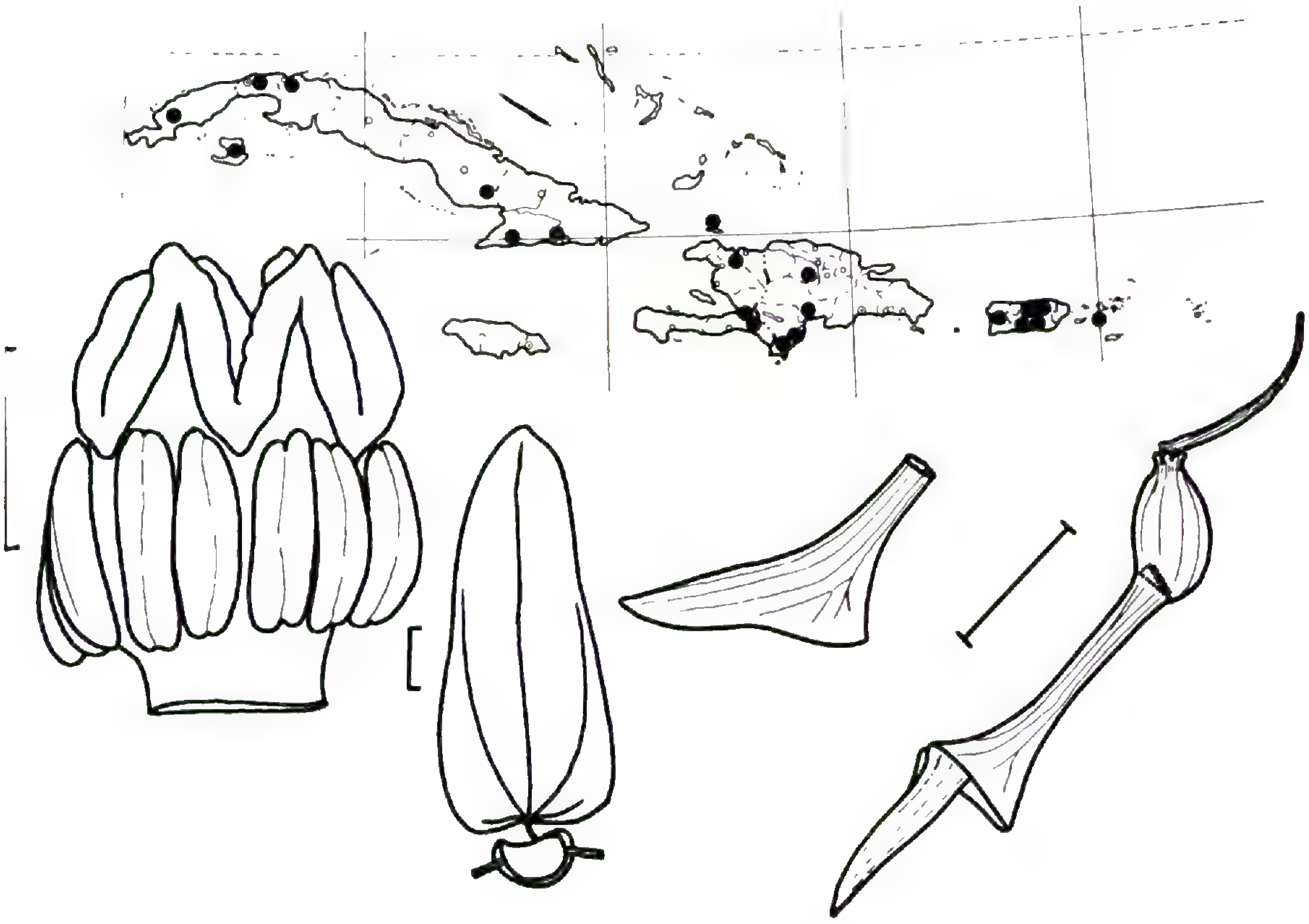


Fig. 45. Gynostemium, distribution, leaf with pseudostipule, portion of flower bud and flower of *A. bilabiata.*

44. Aristolochia caudata Jacq., Enum. Pl. Carib. 30, 1762; Sel. Stirp. Amer. Hist. *t. 145,* 1763, non Booth ex Lindl. (1831), nec Parodi (1878). (ex ic.)—Fig. 46.

Howardia caudata (Jacq.) Klotzsch, Monatsb. Acad. Berlin **1859:** 622, 1859.
Aristolochia brachyura Duchr. in DC., Prod. **15**(1): 446, 1864. (ex char.)
A. punctata Balbis ex Duchr., loc. cit., pro syn.

Subglabrous *lianas. Leaves* triangular-hastate, medially slightly constricted, emarginate to obtuse at the apex, basally deeply cordate-hastate, 2-4 cm broad, 4-6 cm long, minutely hamate-hairy above, beneath glabrous. *Pseudostipules* absent. *Flowers* solitary in the leaf axils, ebracteolate, rectilinear, purple and green, the utricle ellipsoid, 1 cm long, syrinx small, inequilateral flap, the tube straight,

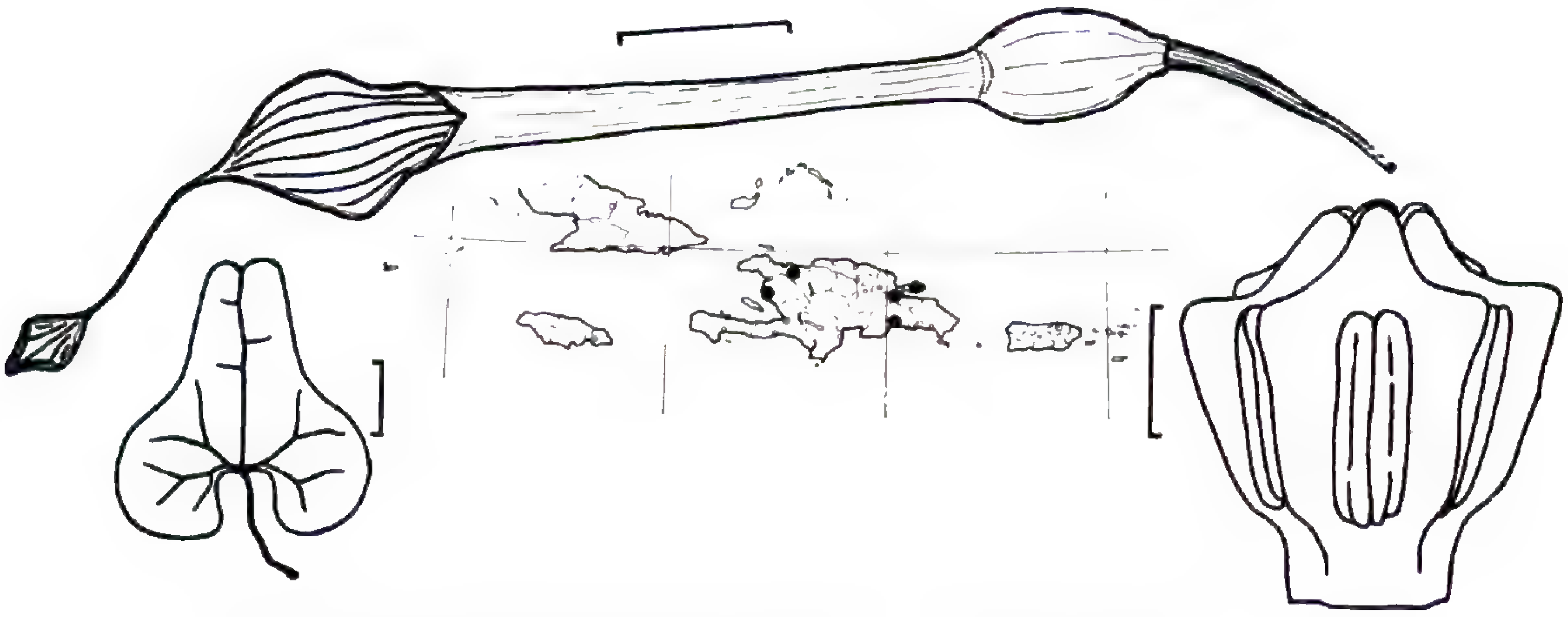


Fig. 46. Flower, leaf, distribution and gynostemium of *A. caudata.*

to 4 cm long, the limb 1-lobed, gradually expanding from the tube, with 2 lateral wings at the base, thence narrowing sharply to a filiform extension which ends in an enlarged, spatulate appendage, 1 cm wide, 3 cm long, inclusively. *Gynostemium* 6-lobed, with 6 radiate wings, 3 mm high, 3 mm broad, the anthers 6, equidistant between the wings. *Fruits* short-cylindric, 2 cm long, 1.5 cm wide, dehiscence acropetal, septifragal, the hypanthium straight, 3 mm long. *Seeds* not seen.

On shrubs in dry, open places, Hispaniola.

HAITI. DOMINICAN REPUBLIC.

The curious caudal appendage distinguishes this species from all others; it is often broken off dried material since it is very fragile.

45. ARISTOLOCHIA EHRENBERGIANA Cham., Linnaea **7:** 209, *t.* 5, 1832. (Type: *Ehrenberg s.n.*, NY)—Fig. 47.

Howardia ehrenbergiana (Cham.) Klotzsch, Montasb. Acad. Berlin **1859:** 622, 1859.

Small, glabrous *lianas*. *Leaves* triangular, slightly emarginate, deeply cordate-sagittate, 1.5-4.5 cm broad, 3-4 cm long, pale green, glabrous. *Pseudostipules* absent. *Flowers* solitary in the leaf axils, ebracteolate, rectilinear, yellowish green and purple, the utricle ellipsoid, 1 cm long, syrinx inequilaterally annular, the tube 2 cm long, the limb 1-lobed, smooth, gradually expanding from the tube, very long-triangular, the appendage becoming filiform thence enlarging slightly into an emarginate, narrowly elliptic terminal lobe, 6 cm long overall. *Gynostemium* 6-lobed, 2 mm high, 2 mm broad, the anthers 6, equidistant. *Fruits* short-cylindric,

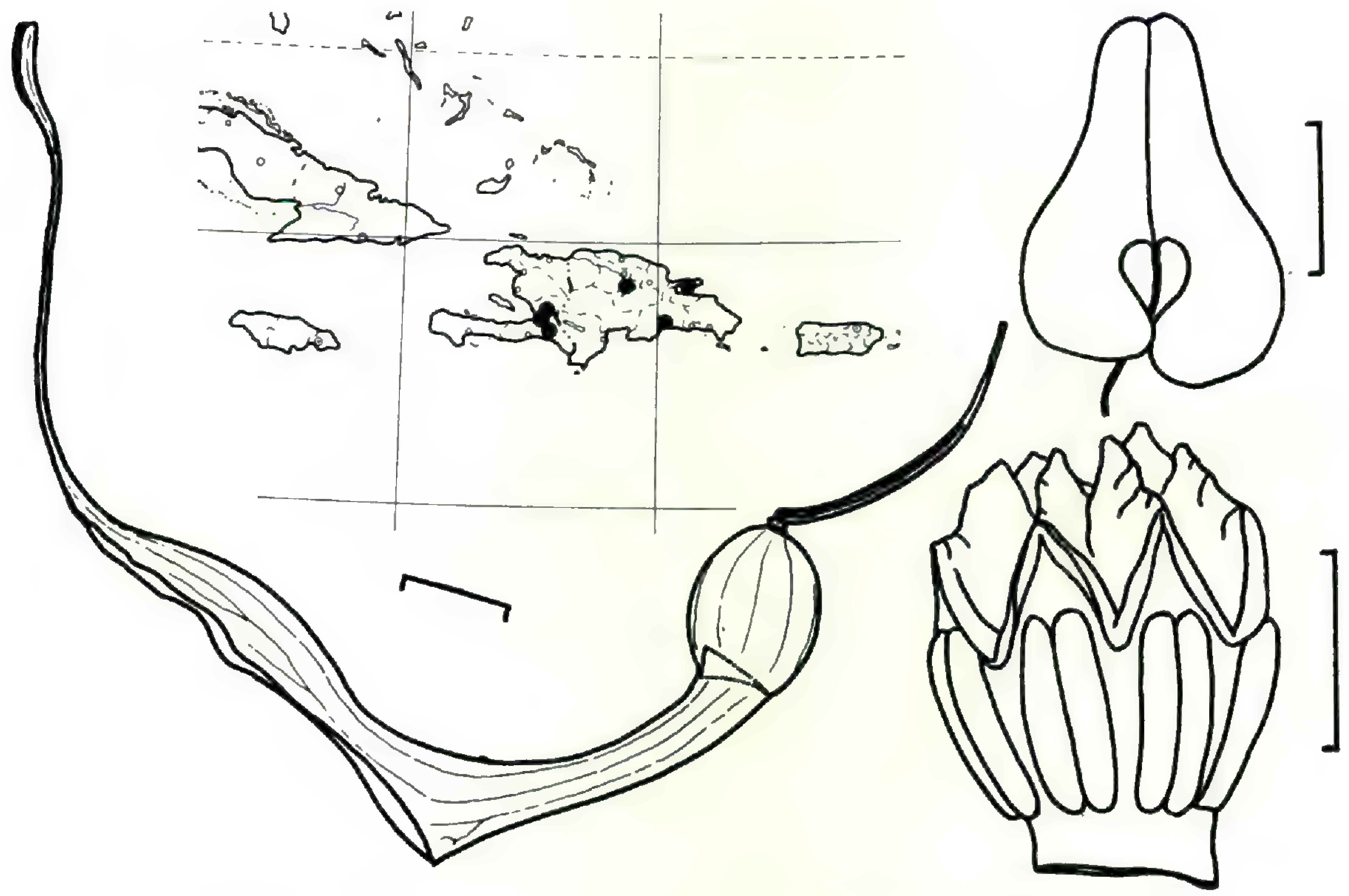


Fig. 47. Flower, distribution, leaf and gynostemium of *A. ehrenbergiana*.

2.5 cm long, 1.5 cm wide, dehiscence acropetal, septifragal, the hypanthium straight, 3 mm long. *Seeds* numerous, flat, 2.5 mm wide, 3.5 mm long, 0.5 mm thick.

On shrubs in dry foothills, Hispaniola.

Haiti. Dominican Republic.

This long-appendaged flower with its curious, small, terminal lobe distinguishes this species from others with similar leaves.

46. Aristolochia clematitis L., Sp. Pl. 962, 1753. (Type: *Linn. Herb. London, no. 1071.11,* photo)

Glabrous perennial *herbs*. *Leaves* broadly cordate, membranous, obtuse at the apex, basally deeply cordate, 6 cm wide, 6 cm long, smooth. *Pseudostipules* absent. *Flowers* in congested axillary fascicles on young stems, ebracteolate, rectilinear, yellow, green and purple, the utricle spheric, 5 mm long, syrinx absent, the tube slightly arcuate, 1 cm long, the limb 1-lobed, triangular, gradually expanding from the tube, 6 mm wide, 7-8 mm long, unappendaged. *Gynostemium* 6-lobed, 2 mm high, 2 mm broad, the anthers 6, equidistant. *Fruits* spheric, 3 cm diameter, dehiscence basipetal, subvalvate. *Seeds* large, flattened, 12 mm wide, 10 mm long, 5 mm thick.

European; said to be naturalized from gardens and on ballast in a few localities, evidently not spreading actively into new areas (Baltimore, Maryland; Philadelphia, Pennsylvania; Boston, Massachusetts; Ithaca, New York and Montreal, Quebec).

Aristolochia clematitis is illustrated in many local floras, taxonomic texts and other works; it is extremely distinct from our own native species.

47. Aristolochia veraguensis Duchr. in DC., Prod. **15**(1): 458, 1864. (Type: *Warcewicz 252;* photos, F, MO, NY, US)—Fig. 48.

Howardia veraguensis Klotzsch ex Duchr., loc. cit., pro syn.
Aristolochia argyroneura Hoehne ex Uribe, Caldasia **7**: 160, 1955. (Type: *Uribe-Uribe 2642*, COL)

Strong, glabrous *lianas*. *Leaves* large, variegated, white along the major veins, heart-shaped, acuminate, deeply cordate-auriculate, 7-12 cm broad, 10-17 cm long, the veins emersed beneath. *Pseudostipules* absent. *Flowers* in basal, cauliflorous, several-branched, racemose clusters, ebracteolate, strongly arcuate, maroon and red, the utricle ovoid, 12 mm long, syrinx, inequilateral, annular-cylindric, the tube arcuate, 22 mm long, the limb 1-lobed, gradually expanding from the tube, lanceolate, smooth, 1 cm wide, 3 cm long, not appendaged. *Gynostemium* 6-lobed, 4 mm high, 3 mm broad, the anthers 6, equidistant. *Fruits* not seen.

In rain forests, Panama and southward.

Panama: Darien, Veraguas.

I know of variegated leaves only in this species. It resembles *A. schippii,* but the latter has larger flowers, not pronouncedly arcuate, and larger, green leaves.

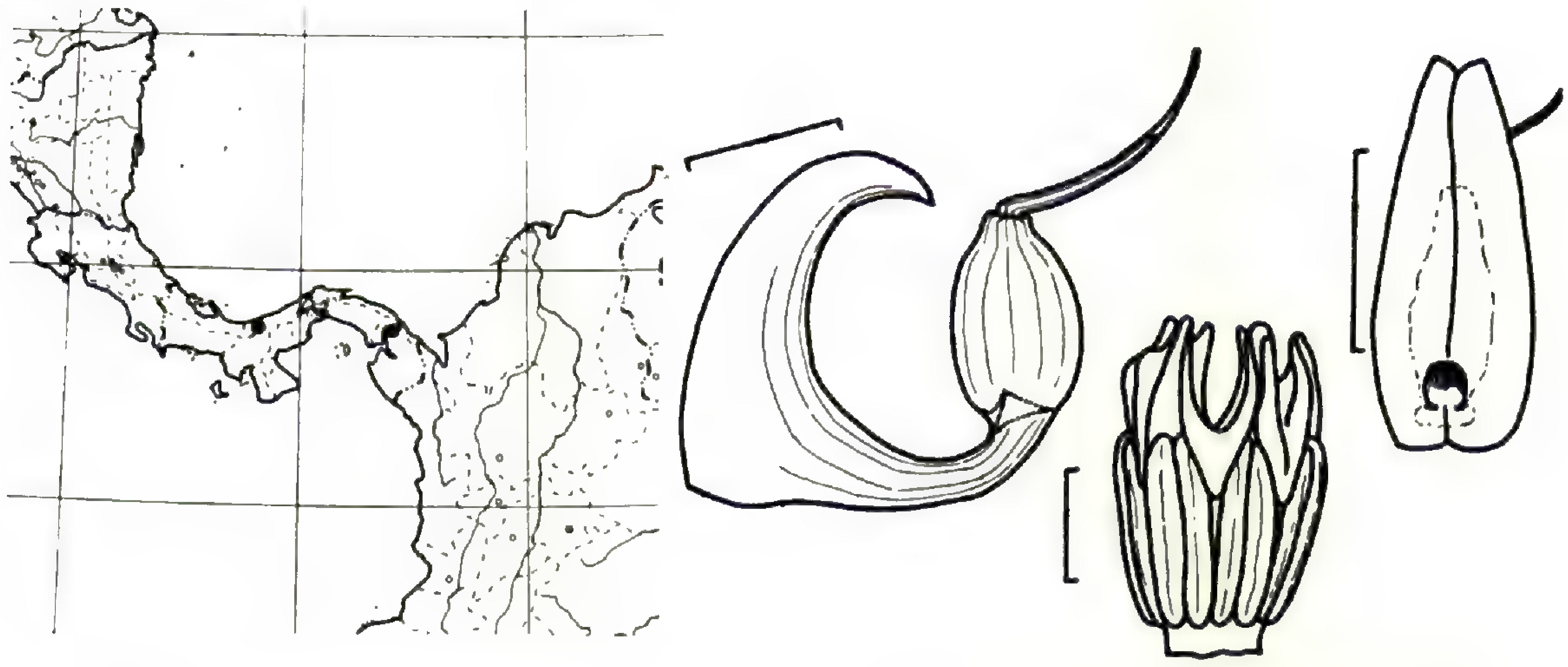


Fig. 48. Distribution, flower, gynostemium and lip detail of *A. veraguensis.*

48. Aristolochia schippii Standl., Field Mus. Pub. Bot. **8:** 8, 1930. (Type: *Schipp* 75, A, F, GH, NY, UC, US)—Fig. 49.

Stout, glabrous *lianas*. *Leaves* large, deep green, heart-shaped, acuminate, deeply cordate, 15-25 cm broad, 18-30 cm long, the veins emersed beneath. *Pseudostipules* absent. *Flowers* in cauliflorous, several-branched, racemose clusters, ebracteolate, rectilinear, mauve, the utricle ovoid, gibbous, 1.5 cm long, syrinx inequilateral, annular-cylindric, the tube rather straight, 2.5 cm long, the limb 1-lobed, gradually expanding from the tube, narrowly triangular, smooth, 3 cm wide, 3.5-4.0 cm long, not appendaged. *Gynostemium* deeply 6-lobed, 5 mm high, 2.5 cm broad, the anthers 6, equidistant. *Fruits* long-cylindric, 13-18 cm long, 2 cm wide, dehiscence acropetal (?), septifragal (?). *Seeds* numerous, flat, 5 mm wide, 5 mm long, 0.3 mm thick.

Along ridges in forests, British Honduras.

British Honduras: Big Creek, Stann Creek.

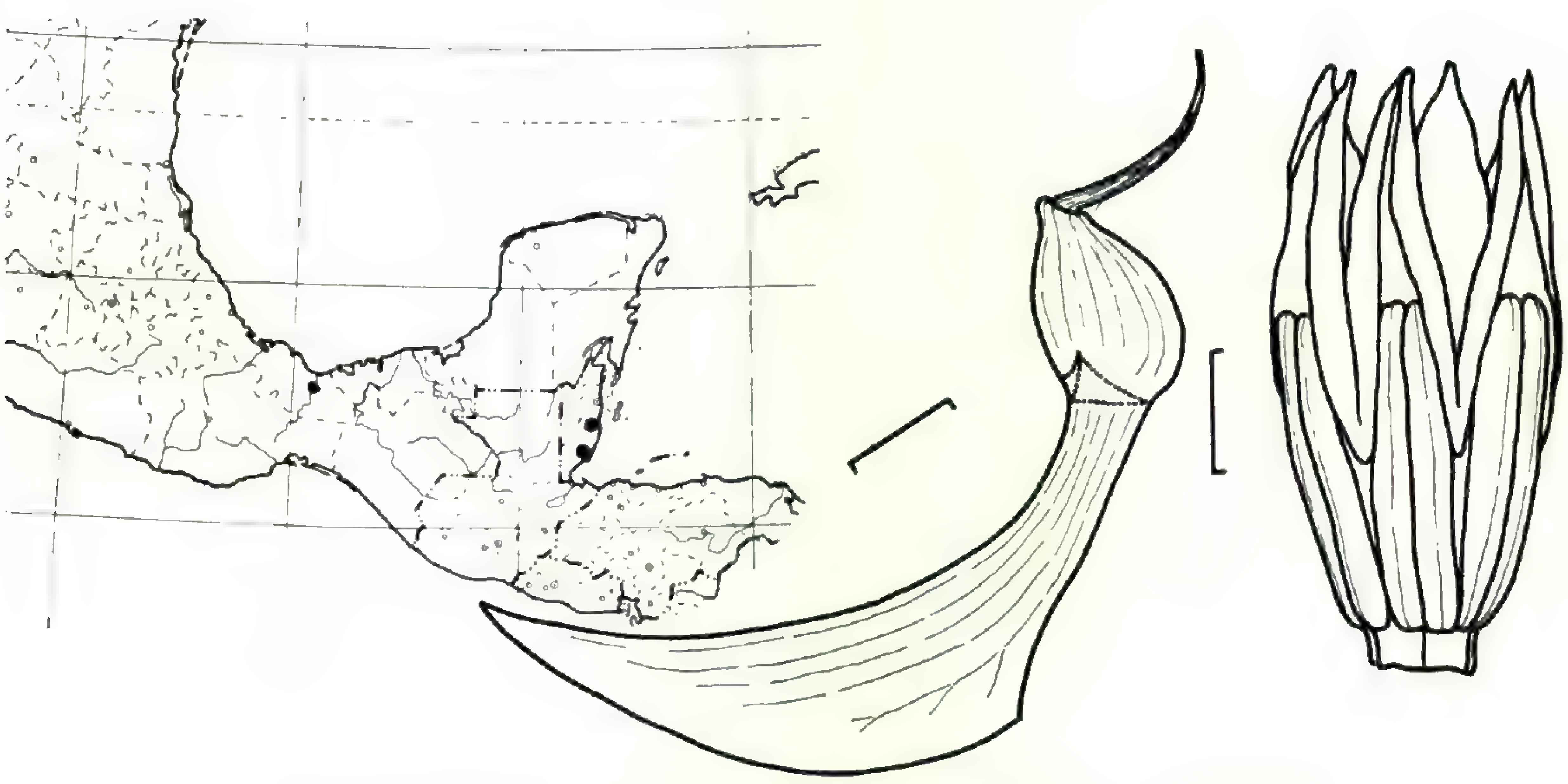


Fig. 49. Distribution, flower and gynostemium of *A. schippii.*

49. Aristolochia inflata H.B.K., Nov. Gen. Sp. Pl. **2:** 145, *t. 111,* 1817. (ex ic.)—Fig 50.

A. odoratissima Benth., Pl. Hartweg. 82, 1841, non L. (1763). (Type: *Hartweg 566,* P; photos, F, MO, NY, US)
A. gibbosa Duchr., Ann. Sci. Nat., sér. 4, **2:** 53, 1854. (Type: *Hartweg 566,* P; photos F, MO, NY, US)
Howardia benthamii Klotzsch, Monatsb. Acad. Berlin **1859:** 620, 1859. (Type: *Hartweg 566,* P; photos, F, MO, NY, US)
H. inflata (H.B.K.) Klotzsch, loc. cit. 619.
Aristolochia torta Willd. ex Klotzsch, loc. cit., pro syn.

Glabrous *lianas*. *Leaves* membranous, broadly triangular, not medially constricted, acute to acuminate, cordate, 3-6 cm broad, 5-8 cm long, green above, paler beneath. *Pseudostipules* present, amplexicaul, orbiculate. *Flowers* axillary, solitary, ebracteolate, rectilinear, faint purple without, inside pale yellow, the utricle extremely gibbous, ovoid, 1 cm long, syrinx an inequilateral, short tube, the tube straight, 1 cm long, the limb 1-lobed, lanceolate, gradually expanding from the tube and about 3 times longer than the tube, 3 cm wide, 3-4 cm long, unappendaged. *Gynostemium* 6-lobed, 2.5-3.5 mm high, 2-4 mm broad, the anthers 6, equidistant. *Fruits* cylindric-fusiform, 2.5-4.0 cm long, 1 cm wide, dehiscence acropetal, septifragal, the hypanthium 3-5 mm long, sharply bent at 90° angle. *Seeds* numerous, cordate, small, flat, 2 mm wide, 2.5 mm long, 0.5 mm thick.

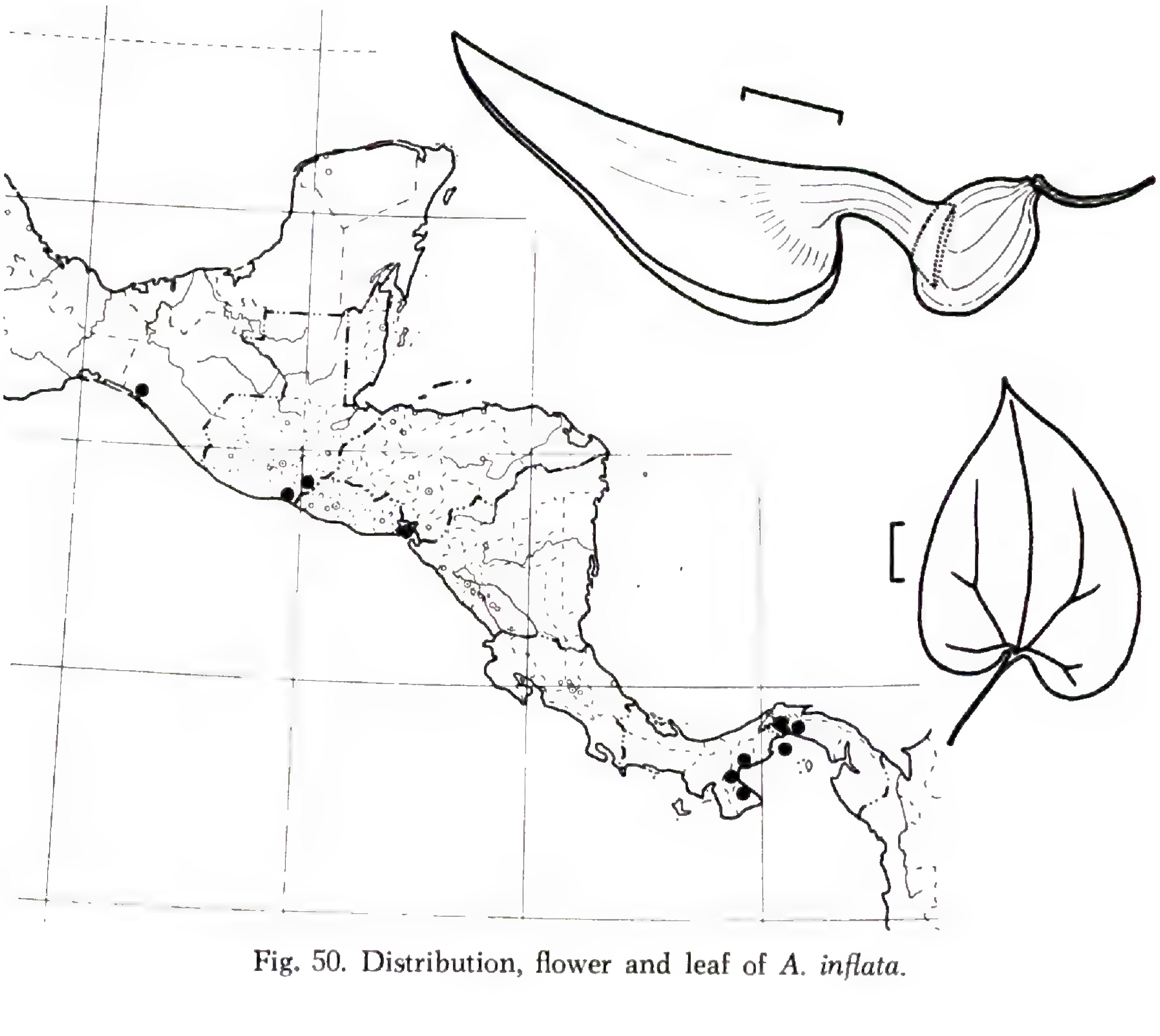


Fig. 50. Distribution, flower and leaf of *A. inflata*.

In thickets and among shrubs; one of the more common species in Central America.

MEXICO: Chiapas.
GUATEMALA: Jutiapa, Santa Rosa.
HONDURAS: Valle.
PANAMA: Aguadulce, Herrera, Panama, Penonomé, Taboga.

Vegetatively this species resembes *A. odoratissima* and *A. littoralis*. It may be distinguished from the former by its smaller flowers and fruits and from the latter by its sharply-curved hypanthium on the fruit tip.

50. ARISTOLOCHIA ANGUICIDA Jacq., Enum. Pl. Carib. 30, 1762, non Pavon ex Duchr. (1864), nec Sieber ex Duchr. (1864). (ex char.)—Fig. 51.

A. mexicana Willd., Sp. Pl. **4:** 157, 1805, non Kostel. (1831), nec A. Dietr. (1839). (ex ic. cit.)
A. pavoniana Duchr., Ann. Sci. Nat., sér. 4, **2:** 55, 1854. (Type: *Pavon s.n.*, FI)
Howardia anguicida (Jacq.) Klotzsch, Monatsb. Acad. Berlin **1859:** 611, 1859.
Aristolochia loriflora Mast. in Engler, Bot. Jahrb. **8:** 220, 1887. (Type: *Lehmann 1702*, F, US)

Glabrous *lianas*. *Leaves* membranous, broadly triangular, acute to obtuse at the apex, basally deeply cordate, 5-7 cm broad, 7-9 cm long, smooth above, beneath with emersed veins. *Pseudostipules* usually present on strong stems, amplexicaul. Flowers solitary in the leaf axils, ebracteolate, rectilinear, purple, green and yellow, the utricle ovoid, gibbous, 1 cm long, syrinx strongly inequilateral, the tube straight, 1.5 cm long, the limb 1-lobed, narrowly triangular, smooth, tightly revolute after anthesis, 1 cm wide, 1.5-2.0 cm long, unappendaged. *Gynostemium* deeply 6-lobed, 3 mm high, 2 mm broad, the anthers 6, equidistant. *Fruits* short, thick-cylindric, 3 cm long, 2 cm wide, dehiscence acropetal, septifragal, the hypanthium 1.5 mm long. *Seeds* numerous, flat, 3 mm wide, 4 mm long, 1 mm thick.

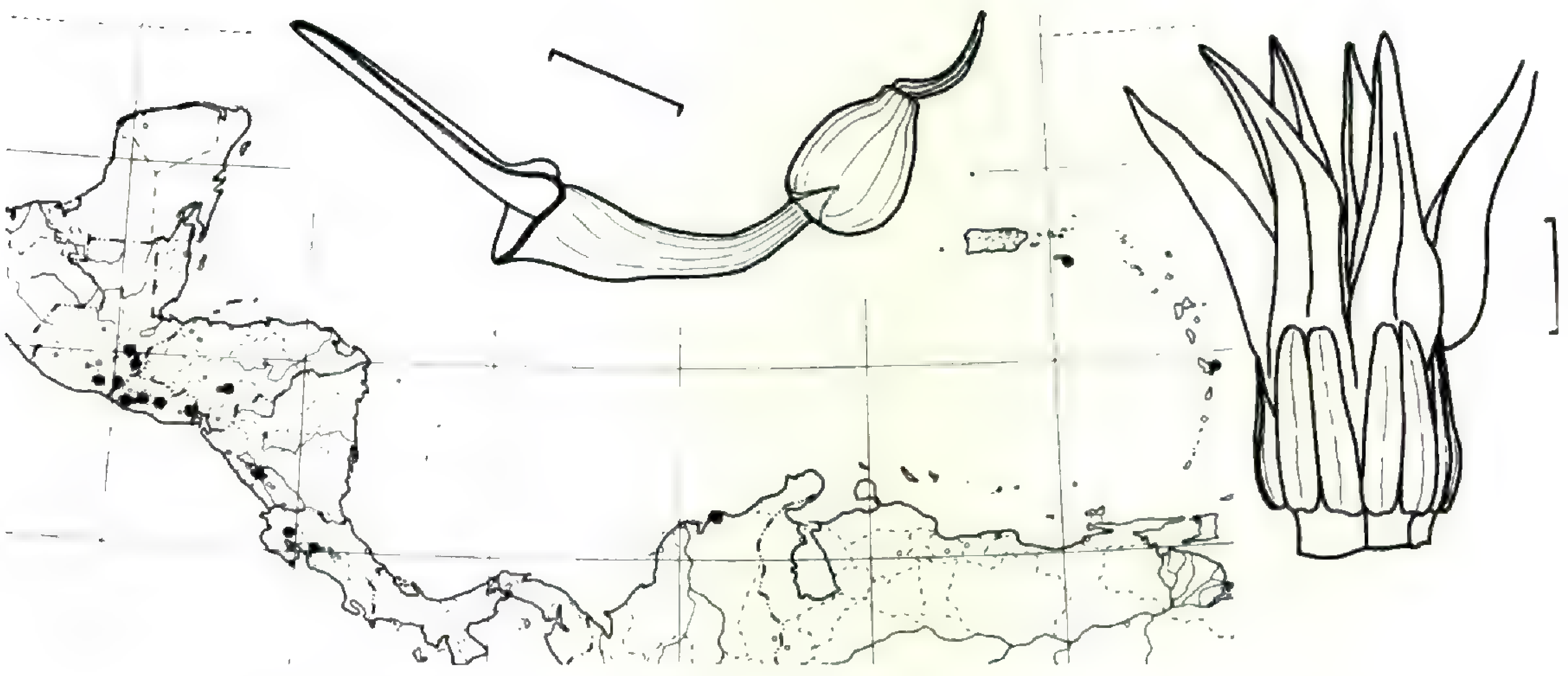


Fig. 51. Distribution, flower and gynostemium of *A. anguicida*.

In damp thickets, Guatemala southward to Costa Rica, and the Lesser Antilles.

GUATEMALA: Chiquimula, Jutiapa, Santa Rosa, Zacapa.
EL SALVADOR: San Salvador, San Vicente, Sonsonate, Unión.
HONDURAS: Morazán.
NICARAGUA: Grenada.
COSTA RICA: Alajuela, Guanacaste.
ST. CROIX. MARTINIQUE.

Vernacular names reported for this plant are *chompipito*, *guaco* and *canastilla;* it is reported to be useful for stomach ache.

51. ARISTOLOCHIA **CARTERAE** Pfeifer, sp. nov.—Fig. 52.

Caules glabri volubiles. *Folia* deltoideo-cordata obtusa basi sagittato-cordata 2-5 cm lata 2-6 cm longa supra glabra subtus nervoso-reticulata. *Pseudostipulae* nullae. *Flores* axillares solitarii ebracteolati subrectilineares purpurei flavi virides; utriculus ovoideus subgibbosus 1 cm longus; syrinx annularis aequilateralis; tuba rectilinearis vel subarcuata circa tam longa quam limbus 2.5 cm longa; limbus 1-lobus lanceolato-ovatus 1.5 cm latus 2.5-3.0 cm longus sine appendice. *Columna* 6-loba obesa urceolata 5 mm alta 5 mm lata; stamina 6 ad libram aequilateralia. *Capsula* subcylindriformis 5 cm longa 2 cm lata basi dehiscens; hypanthium arcuatum 1 cm longum; semina multa plana triangula 4 mm lata 4 mm longa 0.5 mm crassa.—HOLOTYPUS: *Carter & Chisaki 1187*, MO ("vicinity of 'Las Canoas', Rio Cuale, Puerto Vallarta, Jalisco, México, March 26, 1959.") Isotypus: UC.

Glabrous *lianas*. *Leaves* triangular-cordate, obtuse at the apex, basally sagittate-cordate, 2-5 cm broad, 2-6 cm long, smooth above, beneath with emersed venation. *Pseudostipules* absent. *Flowers* solitary in leaf axils, ebracteolate, subrectilinear, purplish streaked with yellow and green, the utricle ovoid, subgibbous,

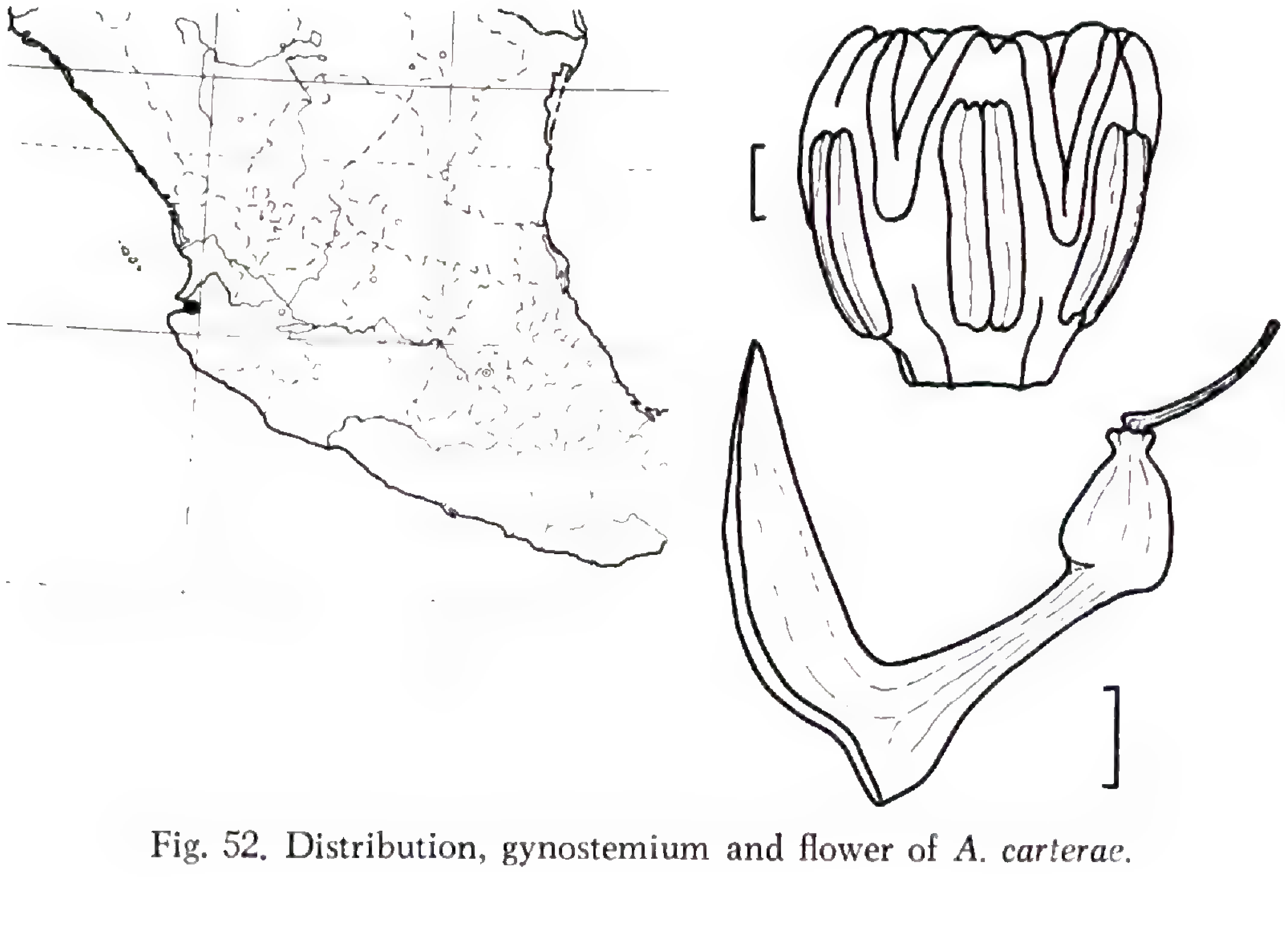


Fig. 52. Distribution, gynostemium and flower of *A. carterae.*

1 cm long, the syrinx inequilaterally annular, the tube straight or slightly arcuate, about as long as the limb, 2.5 cm long, the limb 1-lobed lanceolate-ovate, 1.5 cm wide, 2.5-3.0 cm long, unappendaged. *Gynostemium* 6-lobed, squat, urceolate, 5 mm high, 5 mm broad, the anthers 6, equidistant. *Fruits* cylindric, 5 cm long, 2 cm wide, dehiscing acropetally, the hypanthium arcuate, 1 cm long. *Seeds* numerous, flat, triangular, 4 mm wide, 4 mm long, 0.5 mm thick.

Known only from the type locality.

MEXICO: Jalisco.

Aristolochia carterae is distinguishable from related species by the proportional lengths of the limb and the tube, as well as the distinctive purple and yellow coloration of the limb.

52. ARISTOLOCHIA MONTANA Ekman & Schmidt in Fedde, Repert. Sp. Nov. **29:** 11, 1931. (Type: *Ekman H11840,* S, US)—Fig. 53.

Glabrous *lianas. Leaves* coriaceous, broadly triangular, obtuse to subemarginate, deeply cordate, 4-5 cm broad, 3-7 cm long, beneath with a strong reticulum of raised veins. *Pseudostipules* coriaceous, amplexicaul, orbiculate. *Flowers* axillary, solitary, ebracteolate, arcuate, brown and yellow, the utricle ovoid, 1 cm long, syrinx an inequilateral flap, the tube arched and blending into the limb, 2 cm long, the limb 1-lobed, gradually expanding from the tube, 2 cm wide, 2 cm long, unappendaged. *Gynostemium* subobconic, 6-lobed, 3 mm high, 2 mm broad, the anthers 6, equidistant. *Fruits* not seen.

Known only from type locality.

DOMINICAN REPUBLIC.

This species is sharply distinguished from its near relatives by its coarse leaves, which become leathery and brown after drying.

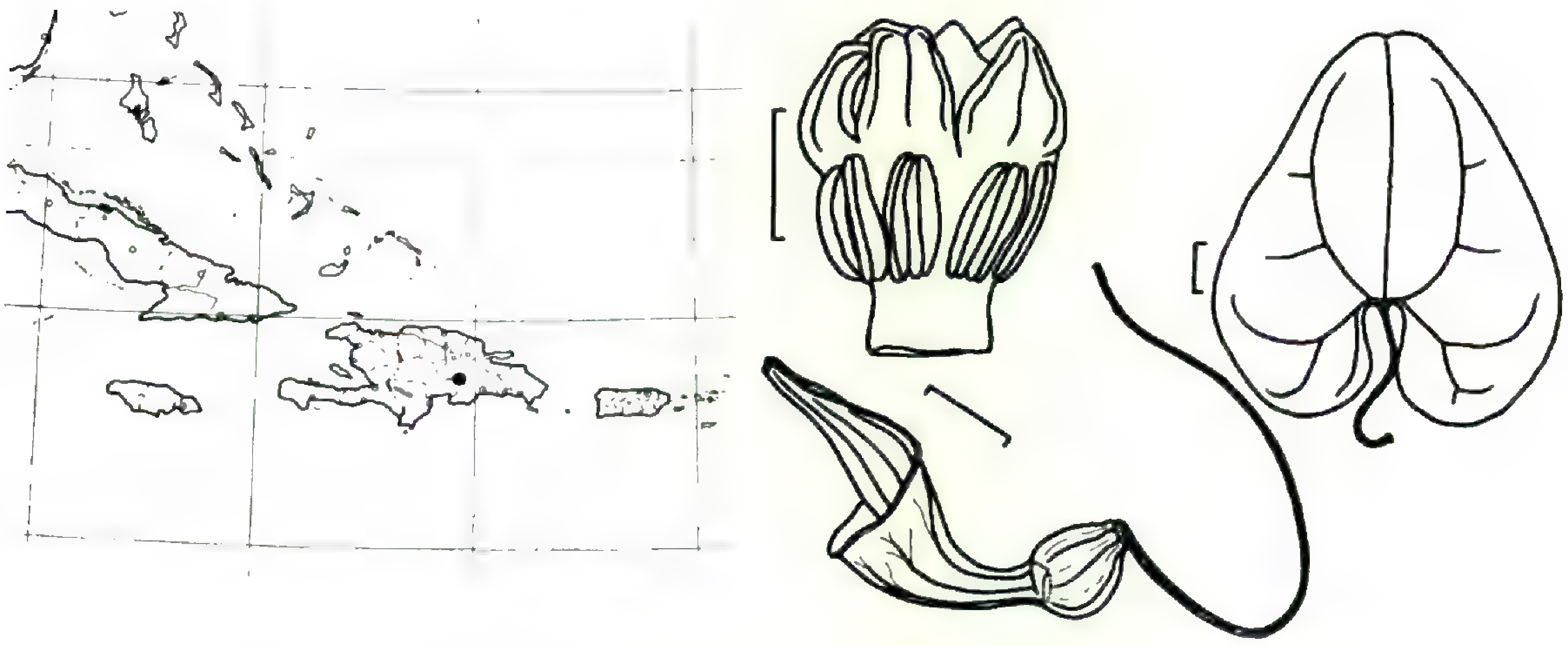


Fig. 53. Distribution, gynostemium, flower and leaf of *A. montana.*

53. ARISTOLOCHIA **GLOSSA** Pfeifer, sp. nov.—Fig. 54.

Caules glabri volubiles. *Folia* suborbiculari-cordata emarginata vel obtusa, basi sagittato-cordata 4-14 cm lata 5-15 cm longa supra viridia subtus pallida nervoso-recticulata. *Pseudostipulae* nullae. *Flores* axillares solitarii ebracteolati rectilineares virides fulvi; utriculus ovoideus 1 cm longus; syrinx annularis inaequalateralis parvula; tuba rectilinearis circa semilongitudo limbi 2 cm longa; limbus 1-lobus spathulatus 1 cm latus 3-4 cm longus sine appendice. *Columna* 6-loba obconica 5 mm alta 3 mm lata; stamina 6 ad libram aequilateralia. *Capsula* cylindriformis 4 cm longa 2 cm lata basi dehiscens; hypanthium rectilineare 4-6 mm longum; semina multa plana triangula 4 mm lata 4 mm longa 0.5 mm crassa.—HOLOTYPUS: *Hinton 15151,* MO ("Aguililla, Apatzingán, Michoacán, México, 1000 m., Sept. 11, 1939."). Isotypi: GH, NY, US.

Glabrous *lianas. Leaves* suborbiculate-cordate, emarginate to obtuse at the apex, basally sagittate-cordate, 4-14 cm broad, 5-15 cm long, deep green above, beneath paler with emersed venation. *Pseudostipules* absent. *Flowers* solitary in leaf axils, ebracteolate, rectilinear, green spotted with brown, the utricle ovoid, 1 cm long, the syrinx unevenly annular, small, the tube straight, about half as long as the limb, 2 cm long, the limb 1-lobed, spatulate, 1 cm wide, 3-4 cm long, unappendaged. *Gynostemium* 6-lobed, obconic, 5 mm high, 3 mm broad, the anthers 6, equidistant. *Fruits* cylindric, 4 cm long, 2 cm wide, dehiscing acropetally,

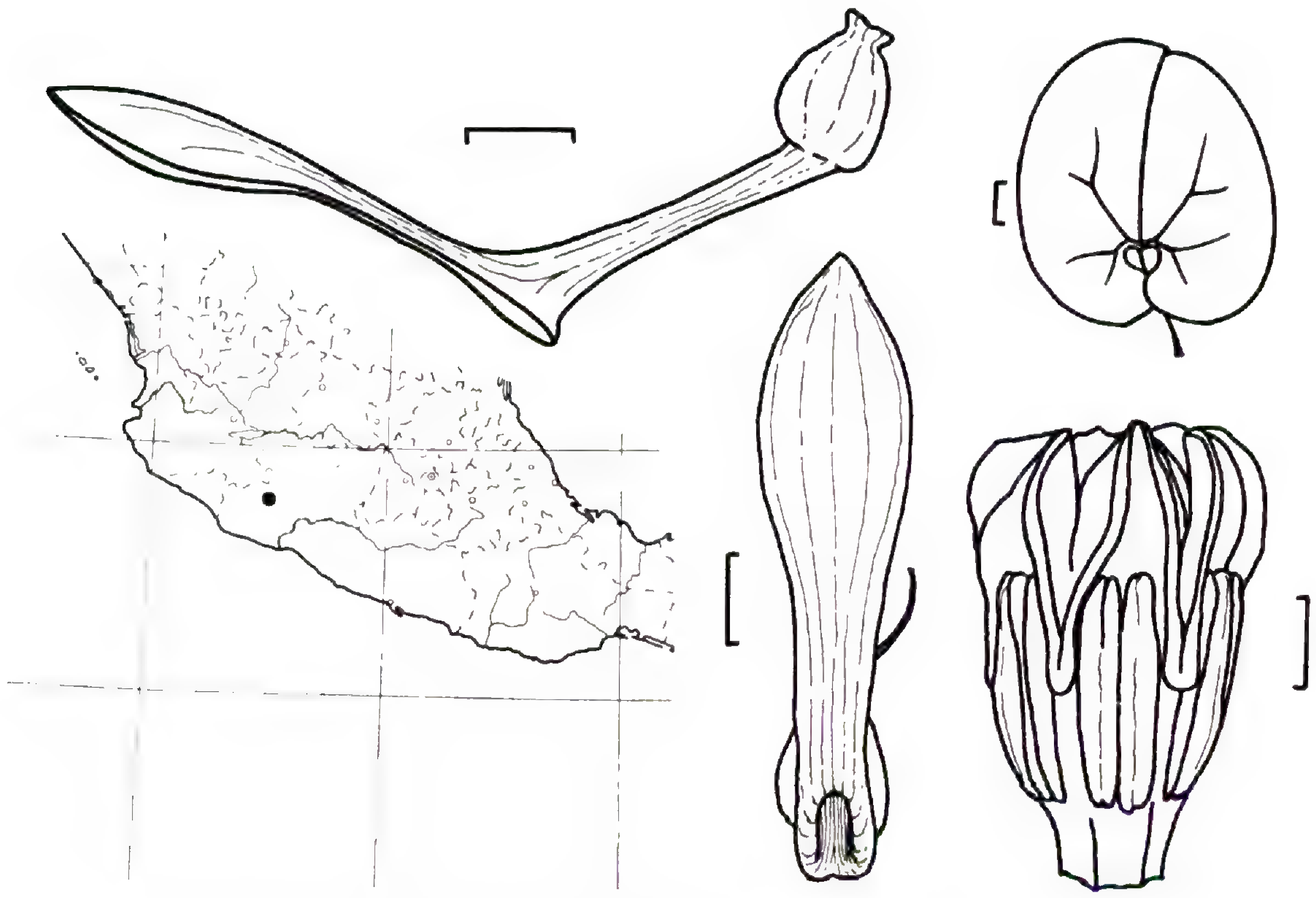


Fig. 54. Distribution, flowers, leaf and gynostemium of *A. glossa.*

the hypanthium straight, 4-6 mm long. *Seeds* numerous, flat, triangular, 4 mm wide, 4 mm long, 0.5 mm thick.

MEXICO: Michoacán.

Sessé & Mociño's collection (no. *4412*, F) labelled *A. longa*, is *A. glossa*. Mrs. Olivia Converse, residing in Valle de Bravo, recently collected this plant from the probable type locality. The generous material which she sent me, together with an original drawing, has greatly aided me in delimiting this species.

Aristolochia glossa is distinguished from *A. taliscana* by its spatulate, efimbriate limb; flowering material of *A. glossa* would not be confused with any other species.

54. ARISTOLOCHIA **MYCTERIA** Pfeifer, sp. nov.—Fig. 55.

Caules subprostrati vel suberecti volubiles. *Folia* deltoideo-cordata obtusa basi cordata 4-10 cm lata 6-12 cm longa supra viridia subtus pallida nervoso-reticulata. *Pseudostipulae* nullae. *Flores* axillares solitarii ebracteolati rectilineares purpurei; utriculus ovoideus gibbosus 1 cm longus; syrinx annularis inaequilateralis; tuba rectilinearis circa tam longa quam limbus 4 cm longa; limbus 1-lobus angustus lanceolati-attenuatus 1 cm latus 5 cm longus, sine appendice. *Columna* 6-loba obesa in anthesi primum urceolata demum obconica circa 5 mm alta 5 mm lata; stamina 6 ad libram aequilateralia. *Fructus* ignotus.—HOLOTYPUS: *Mexia 8790*, MO ("Temisco; Barranca del Consuelo, Guerrero, Mexico; sandy flat above stream, alt. 305 m., frequent; Nov. 11, 1937."). Isotypi: F, GH, NY, S, UC, US.

Glabrous sprawling or prostrate lianas. *Leaves* triangular-cordate, obtuse at

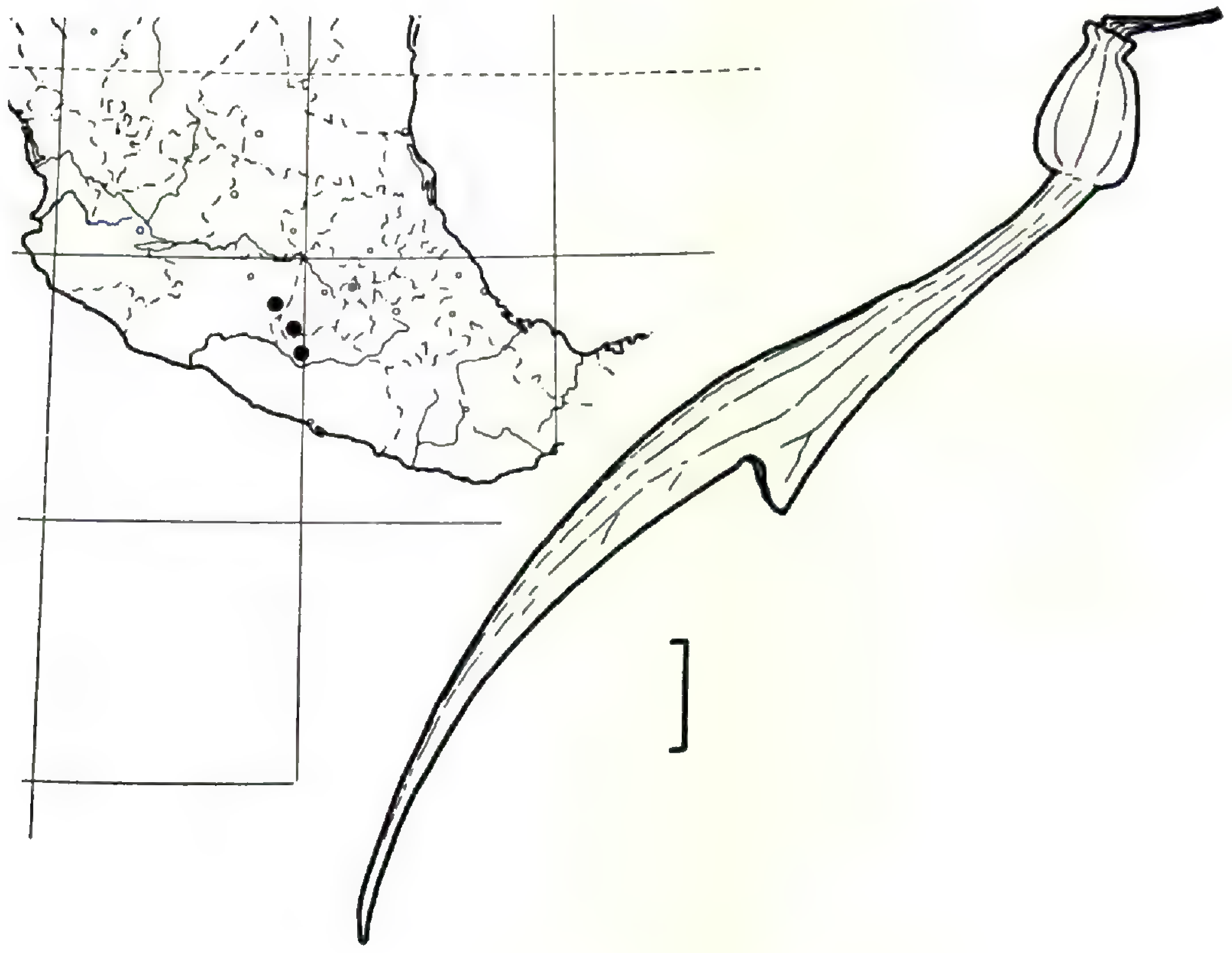


Fig. 55. Distribution and flower of *A. mycteria*.

the apex, basally cordate, 4-10 cm broad, 6-12 cm long, smooth, dark green above, beneath somewhat paler with emersed venation. *Pseudostipules* absent. *Flowers* solitary in leaf axils, ebracteolate, rectilinear, deep purple, the utricle ovoid, gibbous, 1 cm long; the syrinx inequilaterally annular, the tube straight, about as long as the limb, 4 cm long, the limb of the open flower 1-lobed, narrowly lanceolate-attenuate, 1 cm wide, 5 cm long, unappendaged. *Gynostemium* 6-lobed, squat, urceolate when immature, becoming narrowly obconic, ca 5 mm high, 5 mm broad, the anthers 6, equidistant. *Fruits* not seen.

In sandy prairies, often prostrate or growing along stone fencerows.

Mexico: Guerrero, Mexico, Michoacán.

Hinton reports that the sap of the fruit is milky; Miss Mexía notes the vernacular name *hierba del huaco,* and mentions that the decoction made by boiling the roots and stalk is drunk for scorpion sting.

55. Aristolochia chapmaniana Standl., Contrib. Arn. Arb. **5:** 60, 1933. (Type: *Shattuck 413,* F, US)—Fig. 56.

Glabrescent *lianas. Leaves* oblong, acute at the apex, basally cordate, 4-5 cm broad, 10-12 cm long, smooth. *Pseudostipules* absent. *Flowers* solitary in the leaf axils, bracteolate, subarcuate, purple, the utricle narrowly ellipsoid, 5 cm long, syrinx tubular, equilateral, the tube slightly arched, 3 cm long, the limb 1-lobed, narrowly triangular, gradually expanding from the tube, 2 cm wide, 6.5 cm long. *Gynostemium* 6-lobed, 4 mm high, 3 mm broad, the anthers 6, equidistant. *Fruits* large, woody, short-cylindric, 5.5 cm long, 4.5 cm wide, dehiscence acropetal,

Fig. 56. Leaf, distribution, flower and gynostemium of *A. chapmaniana.*

septifragal, the hypanthium absent. *Seeds* numerous, flat, 1.5 cm wide, 9 mm long, 0.75 mm thick.

In rain forests, Panama.

PANAMA: Canal Zone, Coclé, San José.

Vegetatively, *A. chapmaniana* might be mistaken for the common *A. maxima,* but the flowers are very dissimilar. There are plants collected in British Honduras which, vegetatively, closely resemble *A. chapmaniana;* unfortunately they are sterile specimens, precluding positive identification.

56. ARISTOLOCHIA TONDUZII Schmidt in Fedde, Repert. Sp. Nov. **23:** 284, 1927. (Type: *Tonduz 13175,* US)—Fig. 57.

Large, densely tomentulose *lianas. Leaves* elliptic-oblong, apiculate, basally deeply cordate, 5-8 cm broad, 8-15 cm long, green, glabrescent above, beneath darker, densely tomentulose. *Pseudostipules* absent. *Flowers* on short, axillary, bracteolate lateral branches, rectilinear, velutinous, the utricle ellipsoid, 3.5 cm long, syrinx cylindric, equilateral, the tube straight, 3.5 cm long, the limb 1-lobed, gradually expanding from the tube, 2.5 cm wide, 5-6 cm long, on its distal half spotted with elevated maculae. *Gynostemium* 6-lobed, 6 mm high, 3 mm broad, the anthers 6, equidistant. *Fruits* large, woody, 8 cm long, 5 cm wide, dehiscence acropetal, septifragal. *Seeds* numerous, flat, 18 mm wide, 9 mm long, 1 mm thick.

In forests, Costa Rica.

COSTA RICA: Alajuela, Limón, Puntarenas, San José.

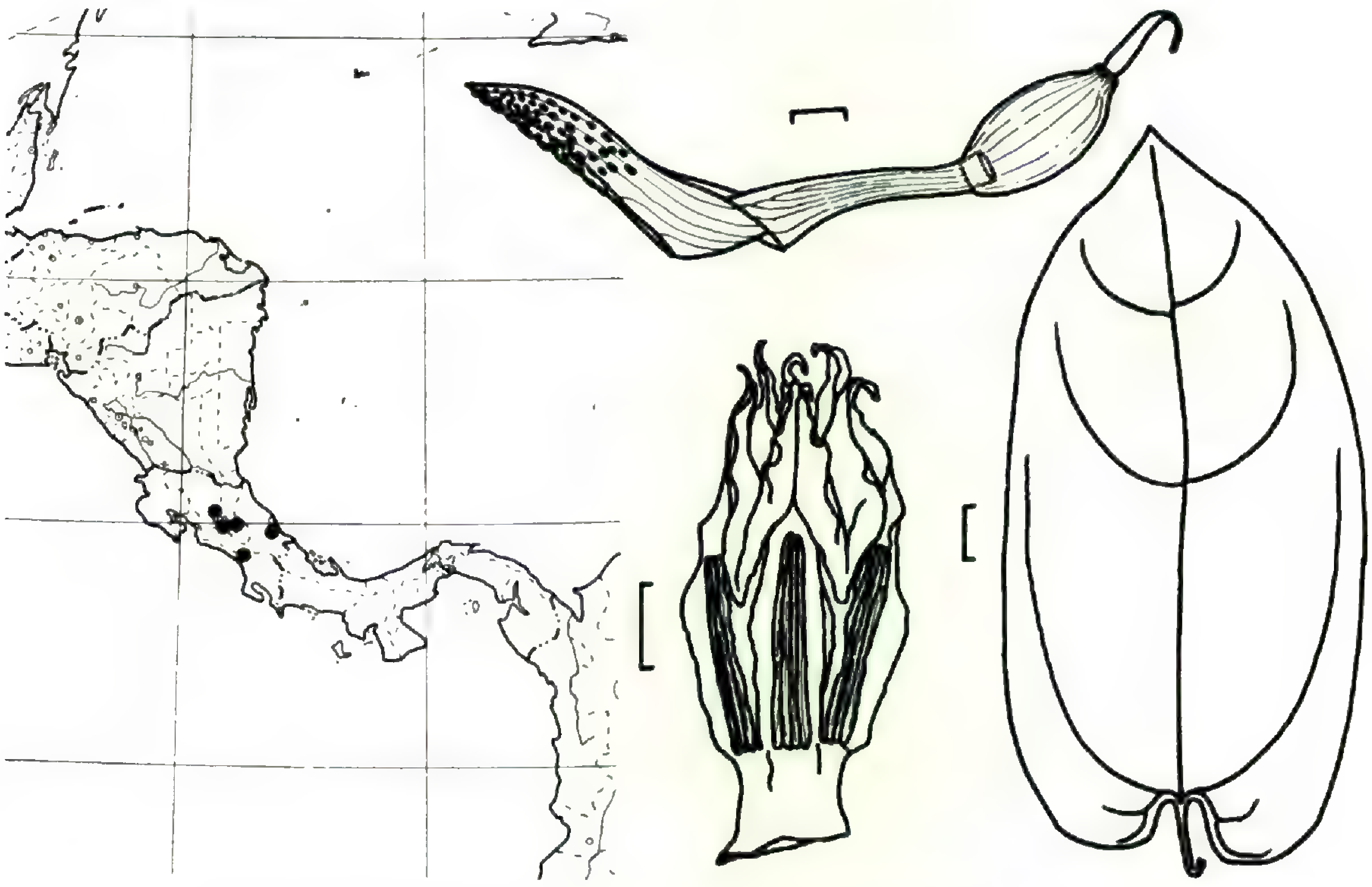


Fig. 57. Distribution, flower, gynostemium and leaf of *A. tonduzii.*

If flowers are present, *A. tonduzii* cannot be confused with any other species. In the past, it has been confused with *A. maxima;* the fruits are similar, but the hairy leaves with cordate bases of *A. tonduzii* should suffice to make the distinction.

Aristolochia reticulata Seem. (Bot. Voy. Herald. 193, 1854) was collected in Tarapota, Peru. The type specimen (BM) is meagre, but suggests close affinities with *A. tonduzii.* Since the name *reticulata* was preempted by Nuttall in 1835, Duchartre renamed the Seemann plant *A. mathewsii* in 1864 in the Prodromus (**15**-1: 497). Unfortunately, he erred in copying the name *reticulata* from Seemann, spelling it *utriculata.* The name *A. tonduzii* is retained here for the North American plant, but with the reservation that *A. mathewsii* Duchr. may be the earlier and correct name. Only further collections will permit the correct assignment of the names, and it will be necessary to review all of the related South American taxa.

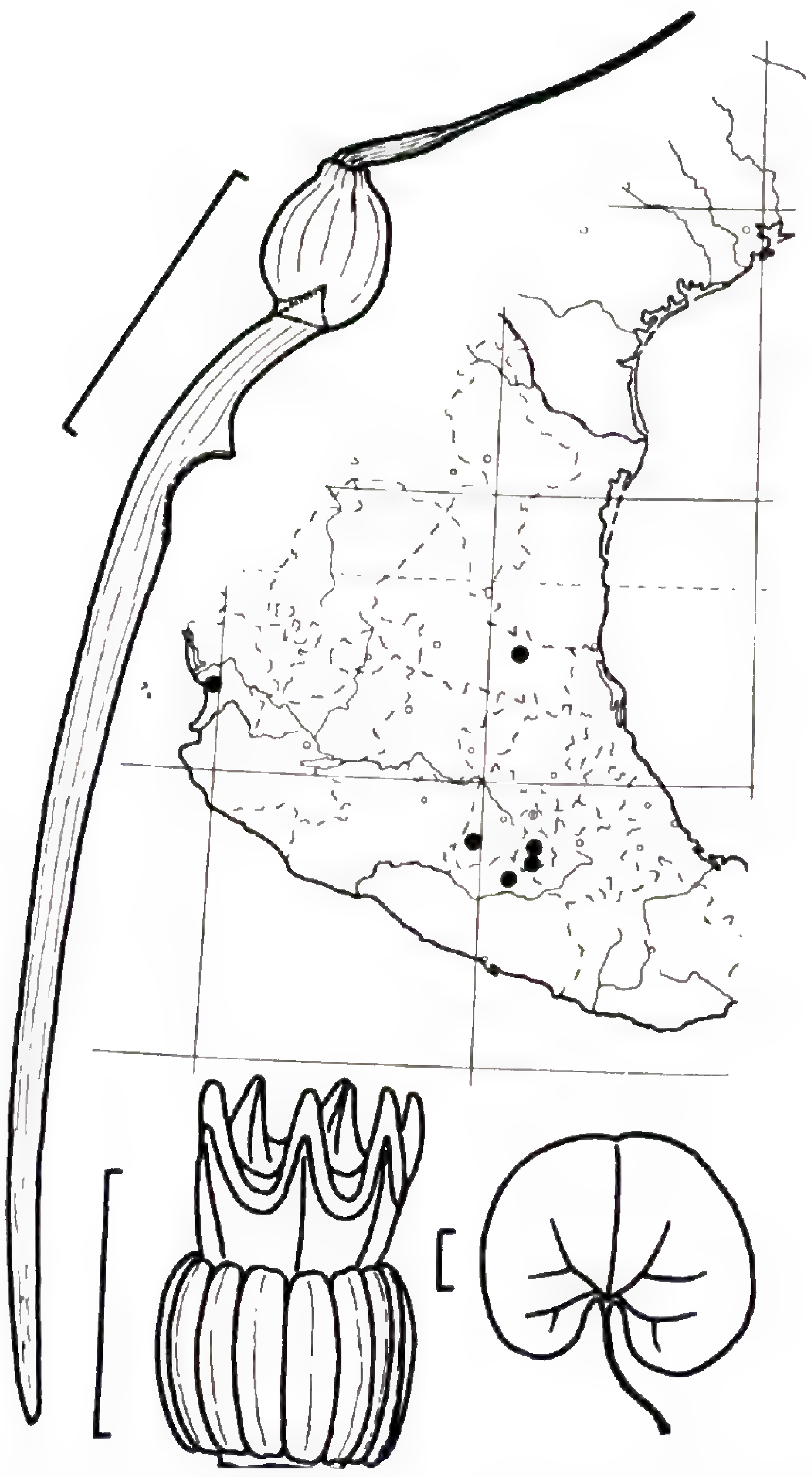


Fig. 58. Flower, distribution, gynostemium and leaf of *A. orbicularis.*

57. Aristolochia orbicularis Duchr., Ann. Sci. Nat., sér. 4, **2:** 59, 1854. (Type: *Sessé &Mociño s.n.;* photos, F, MO)—Fig. 58.

Aristolochia obtusifolia Sessé & Mociño ex Duchr. in DC., Prod. **15** (1): 467, 1864, pro syn.

Suffrutescent, finely puberulent to glabrous perennial *herbs. Leaves* suborbiculate, emarginate to rounded at the apex, basally deeply cordate, 2-7 cm broad, 3-9 cm long, smooth, beneath finely puberulent or glabrous. *Pseudostipules* absent. *Flowers* solitary in the leaf axils, ebracteolate, rectilinear, yellowish-green and dark purple, the utricle subspheric, 5 mm long, syrinx inequilateral, annular, the tube straight, 4 mm long, the limb 1-lobed, linear, 4 mm wide, 3 cm long, subemarginate at the apex. *Gynostemium* 6-lobed, 1.2 mm high, 1 mm broad, the anthers 6, equidistant. *Fruits* ellipsoid, 14 mm long, 11 mm wide, dehiscence basipetal, septifragal. *Seeds* numerous subrevolute, 3mm wide, 4 mm long, 0.2 mm thick.

Rocky slopes, woodlands, Mexico.

Mexico: Guerrero, Mexico, Morelos, Nayarit, San Luis Potosí, Tamaulipas.

This plant is easily identified by the small flowers, and their long, linear limbs, as well as the habit; Hinton reports the Mexican vernacular name *cuajo.*

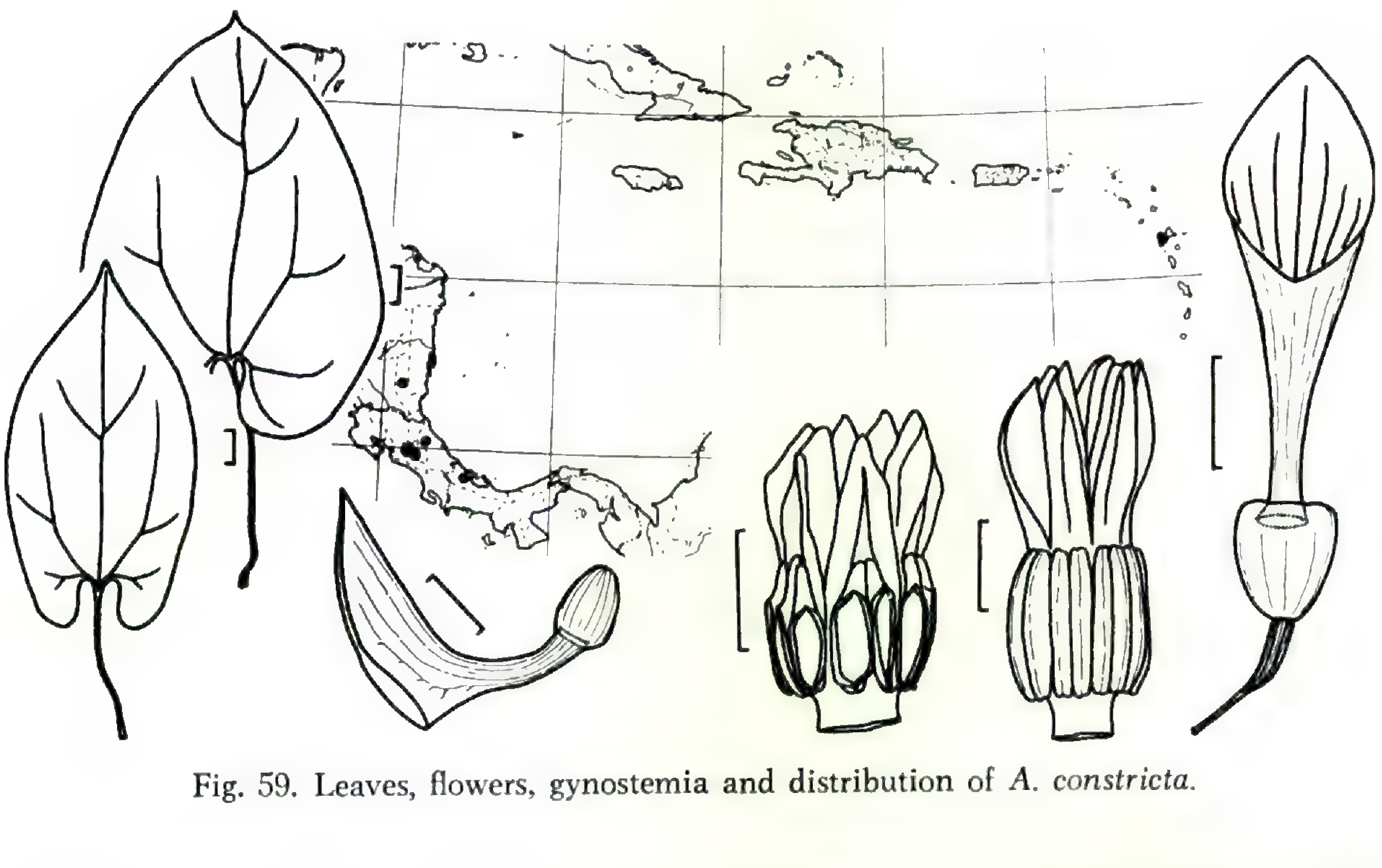


Fig. 59. Leaves, flowers, gynostemia and distribution of *A. constricta.*

58. Aristolochia constricta Griseb., Gesell. Wiss. Goettingen Abh. **7:** 225, 1857. (Type: *Duss 4121,* NY)—Fig. 59.

A. securidata Mast., Bot. Gaz. **33:** 256, 1902. (Type: *Pittier 13422* (JDS 7604), US)

Tomentulose *lianas. Leaves* elliptic to ovate, acuminate, deeply cordate-sagittate, 7-9 cm broad, 10-13 cm long, smooth, dark green above, beneath paler, tomentulose. *Pseudostipules* absent. *Flowers* in short, axillary, several-branched, bracteolate, racemose clusters, rectilinear, purple, the utricle ovoid, 1 cm long,

syrinx cylindric, equilateral, the tube straight, 2 cm long, gradually expanding into the limb, the limb 1-lobed, triangular, ca 1 cm wide, 2.5-3.0 cm long, unappendaged. *Gynostemium* deeply 6-lobed, 3.5 mm high, 2 mm broad, the anthers 6, equidistant. *Fruits* large, ovoid, 6 cm long, 5 cm wide, dehiscence acropetal, septifragal, exposing the latticed septa, the hypanthium absent. *Seeds* numerous, flat, 14 mm wide, 10 mm long, 1 mm thick.

In forests, Costa Rica to Panama, the Lesser Antilles. To be expected in northern South America.

Costa Rica: Cartago, Limón, San José.
Panama: Bocas del Toro.
Guadeloupe.

Excluded Species

Aristolochia arborescens L., Sp. Pl. 960, 1753.
No authentic specimen exists for this species in the Linnaean herbarium. Authors have used *A. arborescens* as a synonym of *A. serpentaria* as well as of *A. grandiflora*. The description as published is inadequate.

A. cubensis J. Linden, Cat. Pl. n. 11, Suppl. **1856:** 12, 1856, nom. nud.

A. dammeriana Mast., Gard. Chron., ser. 3, **17:** 452, 1895.
I have been unable to obtain any material fitting the description of *A. dammeriana*. The Kew herbarium has a species folder bearing this name, but it contains only a cutting of the Gardener's Chronicle article.

A. durior Hill, Veg. Syst. **16:** App. 57, *t. 60,* 1824. = *?Bignonia capreolata* L.
The peculiar circumstances pertaining to Alfred Rehder's acceptance of Hill's epithet, *A. durior* over that of Lamarck (*A. macrophylla*) has been reviewed by me in another paper (Baileya **10:** 4-7, 1962.)

A. leuconeura J. Linden, Belg. Hortic. **8:** 164, 1858.
Based upon sterile material, this is possibly equivalent to *A. veraguensis,* but it is not possible to assign it to that species with certainty. Unfortunately, *A. leuconeura* antedates *A. veraguensis.*

A. longifolia Sessé & Mociño, Fl. Mex., ed. 2, 210, 1894, non Roxb. (1832), nec Hauman (1923).
Impossible to assign from the description, this species is not maintained by any modern authors. A search of the Sessé & Mociño collections from Madrid at Chicago Natural History Museum has failed to turn up any further information. Britton & Wilson, in the Flora of Porto Rico and the Virgin Islands (1924) cite *A. longifolia* as a synonym of *A. oblongata* Jacq. (=*A. bilabiata* L.).

A. podocarpa A. Bert., Acad. Scient. Instit. Bononiensis, Nov. comment. **4:** 437, 1840.
This Bertoloni species was described from leaves and fruits; a search for the type has been unsuccessful. It is possible this species is a synonym of *A. inflata* H.B.K. (1817). The herbarium at Bologna does not have a specimen. The type is from a plant grown from seed collected at Esquintla (=Escuintla), Guatemala by Joachim Velásquez (a member of the Mexican legation at Rome.)

A. pubescens Page ex Steudel, Nom. Bot., ed. 2, **1:** 133, 1840, nom. nud.

A. punctata Lam., Encycl. Méth. Bot. **1:** 253, 1783, non Balbis ex Duchr. (1864).
This species was described by Lamarck who based it upon a plate in Plumier (Spec. 5. Burm. Amer. *t. 34*). Although the species is maintained by Urban (e.g. in Flora Domingensis, Symb. Antill. **8:** 193, 1920), he cited no collections. The type locality is "Anses à Pittes," now Anse à Pitre, Haiti. There are at least three species known from this locality; to judge from the plate, *A. punctata* could be ascribed to any of them, but to no single one with certainty. Futhermore, Hispaniola is rich in species of *Aristolochia,* especially the

southern regions. If one assumes other species may also grow at Anse à Pitre (although not yet collected there), the assignment of the name is even less sure.

A. uhdeana Duchr. in DC., Prod. **15** (1): 465, 1864. (Type: *Uhde s.n.* B†).

The type, the only specimen cited by Duchartre, no longer exists. It is impossible to assign the name with certainty from the description; no other specimens have been seen by me bearing the name *A. uhdeana.*

Enumeration of Hexandrous Species of Aristolochia

1. *A. reticulata* Nutt.
2. *A. serpentaria* L.
3. *A. tricaudata* Lem.
4. *A. malacophylla* Standl.
5. *A. arborea* Linden
6. *A. bullata* Pfeifer
7. *A. paracleta* Pfeifer
8. *A. panamensis* Standl.
9. *A. asclepiadifolia* Brandg.
10. *A. rhizantha* Lundell
11. *A. thwaitesii* Hook.
12. *A. macrophylla* Lam.
13. *A. californica* Torr.
14. *A. tomentosa* Sims
15. *A. trilobata* L.
16. *A. bilobata* L.
17. *A. lindeniana* Duchr.
18. *A. peltata* L.
19. *A. leptosticta* Urban
20. *A. haitiensis* Ekman & Schmidt
21. *A. tentaculata* Schmidt
22. *A. pilosa* H.B.K.
23. *A. taliscana* Hook. & Arn.
24. *A. glandulosa* Kickx
25. *A. clavidenia* Griseb.
26. *A. fuertesii* Urban
27. *A. rugosa* Lam.
28. *A. passifloraefolia* A. Rich.
29. *A. labiata* Willd.
30. *A. ringens* Vahl
31. *A. esoterica* Pfeifer
32. *A. gigantea* Mart. & Zucc.
33. *A. littoralis* Parodi
34. *A. odoratissima* L.
35. *A. grandiflora* Swartz
36. *A. ekmanii* Schmidt
37. *A. tigrina* A. Rich.
38. *A. samanensis* Schmidt
39. *A. maxima* Jacq.
40. *A. chasmema* Pfeifer
41. *A. ovalifolia* Duchr.
42. *A. linearifolia* Griseb.
43. *A. bilabiata* L.
44. *A. caudata* Jacq.
45. *A. ehrenbergiana* Cham.
46. *A. clematitis* L.
47. *A. veraguensis* Duchr.
48. *A. schippii* Standl.
49. *A. inflata* H.B.K.
50. *A. anguicida* Jacq.
51. *A. carterae* Pfeifer
52. *A. montana* Ekman & Schmidt
53. *A. glossa* Pfeifer
54. *A. mycteria* Pfeifer
55. *A. chapmaniana* Standl.
56. *A. tonduzii* Schmidt
57. *A. orbicularis* Duchr.
58. *A. constricta* Griseb.

Literature Cited

Ahles, H. 1959. *Aristolochia serpentaria* var. *nashii* as a new name for *A. serpentaria* var. *hastata.* Jour. Elisha Mitchell Sci. Soc. **75:** 130.

Davis, P. H. & M. S. Khan. 1961. *Aristolochia* in the Near East. Notes Roy. Bot. Gard. Edinburgh **23:** 515-546.

Duchartre, P. 1864. *Aristolochiaceae, In* A. de Candolle, Prodromus syst. natur. regni veget. **15** (1): 421-498.

Hagerup, O. 1961. The perianthium of *Aristolochia elegans* Mast. Bull. Res. Council Israel **10:** 348-351.

Hoehne, F. C. 1927. Monographia illustrada das Aristolochiaceas Brasileiras. Mem. Instit. Oswaldo Cruz **20** (1): 1-111.

Huber, H. 1960. Zur abgrenzung der gattung *Aristolochia* L. Mitteil. Bot. Staatss. München **3:** 531-553.

Klotzsch, F. 1859. Die *Aristolochiaceae* des Berliner Herbariums. Monatsb. Acad. Berlin **1859:** 571-626.

Kupchan, S. M. & R. W. Doskotch. 1962. Tumor inhibitors. I. Aristolochic acid, the active principle of *Aristolochia indica.* Jour. Med. Pharmaceut. Chem. **5:** 657-659.

Lorch, J. 1959. The perianth of *Aristolochia*—a new interpretation. Evolution **13:** 415-416.

Petch, T. 1924. Notes on *Aristolochia.* Ann. Roy. Bot. Gard. Peridеniya, Ceylon **8:** 1-108.

Schmidt, O. C. 1935. *Aristolochiaceae, In* A. Engler & K. Prantl, Nat. Pflanzenfam., ed. 2, **16b:** 202-242.

Index to Exsiccatae

Parenthetical numerals refer to the numbers of the species conserved in this revision.

Abbott 1944, (43), *3061* (16). *Abrams 1584* (13). *Acuña 12403* (17). *Adams & Wherry 2361* (12). *I Aguilar 299* (39), *415* (4), *475* (5). *J. I. Aguilar 1569* (50). *M. H. Aguilar 481* (34). *Ahles 12084* (2) *15262* (2), *41903* (2), *45457* (2). *Aiken s.n.* 5 May 1896 (2). *Bro. Alain, 2759* (37). *Alfaro s.n.* 27 July 1925 (2). *Allard 3609* (12), *11518* (12), *12228* (30), *14795* (30), *14928* (45), *16172* (30), *18036* (30), *18080* (30). *C. Allen, 240* (22). *P. H. Allen, 291* (35), *864* (22), *867* (35), *1101* (49), *2032* (49), *2210* (47), *2250* (32), *4021* (39), *4292* (35), *5040* (8), *5767* (39). *Ames s.n.* ann. 1888 (13), *s.n.* March 1891 (13). *E. K. Anderson, s.n.* ann. 1893 (13). *W. A. Anderson, & Jennison 853* (12). *Ark s.n.* (14). *Armour 68* (35). *Aschman s.n.* (2). *Audubon s.n.* (2). *Austin 151* (13), *1794* (13), *s.n.* ann. *1883* (13). *Aviles 70* (22).

Bachman s.n. 18 Aug 1910 (2). *Bacigalupi 2232* (13). *Bain 17* (2), *449* (14). *Baker, C. F. 92* (29), *7272* (33). *M. S. Baker, s.n.* 17 May 1900 (13). *Ball s.n.* ann. 1890 (12). *Bangham 455* (55). *Barkley, Rowell & Webster 2318* (57). *Bartholomew 226* (12). *Bartlett 12936* (35), *s.n.* 6 July 1904 (2). *Bartram s.n.* 31 May 1909 (12). *Basil s.n.* July 1837 (12). *Bass s.n.* 5 October 1938 (14). *Bauer 58* (2). *Beard 1573* (2). *Beardslee s.n.* 5 Aug 1891 (12), *s.n.* 10 Aug 1891 (12). *Beardslee, & Kofoid s.n.* 5 Aug 1891 (12). *Beaupertuis s.n.* ann. 1839 (27). *Beauvoir s.n.* (2). *Bebb s.n.* (2). *Belanger 269* (35), *504* (34), *505* (39). *Berkley 1083* (12). *Bernoulli 11* (50). *Bicknell 3698* (2), *3699* (2), *3700* (2). *Bidwell s.n.* Feb 1879 (13), *s.n.* Feb. 1885 (13). *Biedlé s.n.* (15), *s.n.* (16), *s.n.* (18), *s.n.* (43). *Bigelow s.n.* ann. 1853-4 (13), *s.n.* ann. 1853-4 (14). *Billberg s.n.* Apr 1826 (35). Biltmore Herbarium 75 (2), 75a (2), 75b (2), 75c (2), 75d (2), 75e (2), 75f (2), 75g (2), 75h (2), 75i (2), 75j (2), 75k (2), 751 (2), 75m (2), 75n (2), 75o (2), 75q (2), 75r (2), 75s (2), 75t (2), 1132a (14), 1132b (14), 1132c (14), 1132d (14), 1329 (12), 1329a (12), 1329b (12), 1329c (12), 1329d (12), 1329e (12), 4782 (1) 6144 (2), 6144b (2), 6144c (2), 6144d (2), 6144e (2), 6144f (2), 6152h (14), 9987 (2), 9987b (2), 9987c (2), 9987d (2), 9987e (2), 14782 (1), *s.n.* Jan 1900 (2), *s.n.* 30 June 1900 (2), *s.n.* (2). *Bioletti s.n.* May 1891 (13). *Blake 7493* (35). *Blankinship s.n.* 29 Apr 1893 (13). *Blanton 6651* (33). *Bodin 210* (14). *Bonpland 9373* (50). *Botteri 157* (35). *Bower s.n.* 30 May 1876 (12), *s.n.* (12), *s.n.* (14). *Box 645* (33), *s.n.* 29 May 1938 (15). *Boykin s.n.* ann. 1836 (2). *Boynton s.n.* May 1899 (2). *Brace 6920* (28), *6967* (28), *7109* (28). *Bracelin 1953* (13). *Brandegee s.n. 19* Apr 1916 (13). *Brenckle 47-424* (35). *Brenes 5461* (56), *14292* (56), *14293* (22), *15706* (47), *17287* (22), *17508* (22), *22460* (50), *s.n.* 4 Sept 1932 (22), *s.n.* ann. 1903 (22). *Brewer 919* (13). *Bright 6284* (12), *14661* (12), *14674* (12). *Brinton s.n.* 8 June 1890 (2). *Britton, E. G. 2947* (35), *3298* (28). *Britton E. G. & Marble 386* (15). *N. L. Britton, 2360* (28), *4065* (35), *4125* (15), *s.n.* 24 June 1882 (12), *s.n.* 21 June 1882 (14), *s.n.* 21 Sept 1887 (2), *s.n.* 1 July 1902 (2). *Britton & Britton 199* (15), *200* (34), *7129* (43) *7850* (30). *Britton, Britton & Brown 6781* (43). *Britton, Britton & Cowell 13104* (28), *13150* (28), *13198* (30). *Britton, Britton, & Gager 7391* (37). *Britton, Britton & Vail s.n.* 1 May 1892 (2), *s.n.* 29 May 1892 (12), *s.n.* 11 June 1892 (2). *Britton, Britton & Wilson 6085* (28), *14006* (28), *15006* (43). *N. L. Britton, & Brown 5517* (15). *N. L. Britton, & Cowell 787* (33), *10189*

(28), *12740* (43). *N. L. Britton, Cowell & Earle 10285* (28). *N. L. Britton, Cowell & Shafer 12969* (17). *N. L. Britton, & Earle 7608* (37). *N. L. Britton, Earle & Gager 6874* (24). *N. L. Britton, Earle & Wilson 6243* (37). *N. L. Britton, & Hollick 2134* (35). *N. L. Britton, & Millspaugh 3009* (28). *N. L. Britton, & Shafer 388* (34), *583* (15), *739* (15). *N. L. Britton, & Wilson 125* (43), *143* (37), *297* (24), *5518* (37). *N. L. Britton, Wilson & Bro. León 15297* (24). *Broadway 5202* (35), *7848* (35), *9233* (5), *s.n.* 26 Aug 1932 (35), *s.n.* ann. 1925 (35). *Brown, Hogg, Vail, Timmerman, Britton & Britton s.n. 2 June 1890* (12). *G. M. Brown, s.n. 15 May 1913* (14). *M. Brown, s.n.* Aug 1955 (2). *R. W. Brown, s.n.* 11 Aug 1877 (2). *S. Brown, & N. L. Britton 1605* (15), *1616* (33). *S. Brown, N. L. Britton, & Bisset 2014* (50). *Bruce 1794* (13). *Bucher 101* (17), *110* (17). *Buckholz s.n.* Nov 1922 (14). *Buckley s.n.* May 1841 (2), *s.n.* May 1891 (2), *s.n.* June 1838 (12), *s.n.* May 1839 (14), *s.n.* June (14), *s.n.* ann. 1853 (14), *s.n.* (14). *Burchard s.n.* 29 Sept. 1938 (14). *Burk s.n.* (2). *Bush 24* (2), *120* (2), *187* (2), *196* (2), 333 (2), *494* (2), *560* (14), *724* (2), *775* (14), *898* (14), *982* (1), *2393* (1), *2402* (1), *2450* (2), *2702* (2), *5200* (2), *5715* (2), *5716* (1), *6205* (2), *6373* (2), *7851* (14), *15813* (14), *s.n.* 24 July 1891 (14), *s.n.* 17 May 1892 (2), *s.n.* 24 July 1892 (2), *s.n.* 13 Aug 1892 (2), *s.n.* 14 Aug 1892 (2), *s.n.* 15 Sept 1893 (2). *Buswell s.n.* 30 Jan 1950 (34).

Cain 556 (12). Calderón *148* (50), *197* (50), *287* (5), *441* (39), *442* (50), *702* (35), *1096* (5), *1484* (5), *2480* (39). *Camp 1524* (12), *1565* (12). *Canby s.n.* Aug.-Sept. 1878 (2), *s.n.* May 1869 (12), *s.n.* June 1876 (12). *Canby & Sargent 86* (2). *Carter 1040* (13). *Carter & Chisaki 1187* (51). Casstromii Herbarium *s.n.* (15). *Cathcart s.n. 29* May 1892 (12). *Chandler 866* (13), *7599* (13). *Chapman 32* (2), *s.n.* (2), *s.n.* (12), *s.n.* (14). *Chestnut s.n.* July 1893 (13). *Chestnut & Drew s.n.* 21 Mar 1891 (13), *s.n.* 15 Apr 1889 (13). *Chickering Jr. s.n.* 11 May 1903 (2). *Churchill s.n.* 26 May 1889 (2). *Bro. Clément 2501* (30), *4255* (43), *6096* (17). *Clokey 2422* (2). *Coker s.n.* 7 Sept. 1940 (2). *Collins 18* (35). *Combs 488* (28), *760* (28). *Commons s.n.* 2 July 1868 (2), *s.n.* 3 Aug 1868 (2), *s.n.* 14 July 1873 (2), *s.n.* 1 June 1873 (12). *Congdon s.n.* 22 May 1892 (13), *s.n.* 4 Apr 1894 (13). *Converse 46* (33), *96* (53). *Conzatti & Gonzales 1181* (35). *M. T. Cook s.n.* 10 July 1906 (29), *s.n.* July 1906 (33). *O. F. Cook, & Griggs 22* (35), *182* (35). *Copeland 3044* (13). *Cory 21830* (1), *21890* (2), *21892* (1), *34710* (2), 38892 (2), *s.n.* 24 Sept. 1939 (2). *Coulter 1413* (23), *s.n.* (2), *s.n.* (23). *Craig s.n.* 12 Apr 1911 (33). *Crawford s.n.* 12 Apr. 1897 (2), *s.n.* (2). Crocket *s.n.* (1). *Crooke s.n.* 23 June 1873 (2). *J. T. Curtis Jr. s.n* 31 Dec 1943 (33). *M. C. Curtis s.n.* (1). *Curtiss 4993* (2), *6394* (14), 7538 (2), 7539 (12), *10654* (14), *s.n.* 1 June 1872 (2), *s.n.* June 1873 (2), *s.n.* June 1872 (2), *s.n.* 1 July 1867 (2), *s.n.* (2), *s.n.* 13 June 1872 (12), *s.n.* June (12), *s.n.* ann. 1875 (14). *Cuthbert 157* (2).

Deam 36 (22), *158* (35), *16745* (2), *17424* (2), *s.n.* 25 Dec 1898 (22). *Demaree 5613* (14), *6680* (14), *8513* (14), *8840* (14), *9452* (14), *20138* (14), *20652* (14), *23506* (14), *34983* (2). *Demetrio s.n.* May-June 1886 (2). *Denny s.n.* 6 Nov 1852 (14), *s.n.* ann. 1852 (14). *Denslow s.n.* Sept 1847 (2). *Dettwiller s.n.* ann. 1837 (2). *Dodge 8312* (30). *Dowell 1753* (2), *3936* (2). *Drake s.n.* (15), *s.n.* ann. 1852 (29), *s.n.* (29). *Dressler 1078* (23). *Dressler & Wirth 2701* (23), *2724* (57), *2746* (21). *Drummond 226* (1). *Drushel s.n.* 22 July 1914 (2), *s.n.* 13 May 1916 (14). *Duchassing s.n.* (15), *s.n.* ann. 1851 (49). *Dudley 107* (46), *s.n.* 31 Mar 1894 (13), *s.n.* 11 May 1901 (13), *s.n.* 7 May 1904 (13). *Dugès s.n.* ann. 1880 (23). *Dukes s.n.* ann. 1905 (2). *Duncan 7585* (12). *Dunlap 18* (22), *247* (32), *420* (22), *555* (34). *Durand s.n.* (2). *Père Duss 48* (27), *89* (27), *151* (34), *582* (15), *627* (27), *628* (15), *629* (27), *887* (50), *2104* (35), *2585* (15), *2957* (27), *3573* (27), *3660* (58), *3862* (29), *3890* (58), *3962* (33), *4048* (27) *4121* (58), *4668* (27) *4725* (50). *Dyer A88* (22), *A130* (22), *A144d* (35).

A. J. Eames *s.n.* 20 May 1942 (46). *A. J. Eames, Gershoy & Wiegand 9830* (46). *E. H. Eames 95* (2), *10656* (12). *Earle & Baker s.n.* 5 June 1897 (2). *Eastwood 1474* (13), *s.n.* 26 May 1897 (13). *Eby s.n.* ann. 1897 (2). *H. Edwards s.n.* Apr 1877 (13). *J. B. Edwards 369* (39). *Eggers 1676* (15), *1837* (16), *4974* (28), *s.n.* 30 Apr 1876 (15), *s.n.* 21 May 1876 (15), *s.n.* 19 June 1876 (15), *s.n.* 21 Nov 1875 (15). *Eggert s.n.* 15 May 1896 (2), *s.n.* 19 May 1877 (14), *s.n.* 18 June 1877 (14), *s.n.* 15 May 1879 (14), *s.n.* 19 May 1879 (14), *s.n.* 7 July 1893 (14), *s.n.* 28 May 1875 (14). *Ehrenberg s.n.* ann. 1839 (45). *Ekman 324* (28), *506* (24), *835* (43), *1159* (37), *1163* (28), *1298* (43), *2232* (17), *3212* (17), *3226* (28), *4743* (17), *5186* (43), *5852* (33), *6480* (30), *7815* (43), *8947* (17), *9714* (17), *12913* (37), *13382* (28), *13398* (28), *13605* (24), *13871* (24), *16549* (37), *16891* (37), *17221* (43), *18225* (43), *19035* (28), *H64* (19), *H309* (16), *H836* (19), *H975* (45), *H1059* (16), *H2018* (45),

H2091 (45), *H2377* (19), *H2443* (42), *H2632* (43), *H2763* (33), *H2885* (15), *H3420* (43), *H3826* (18), *H4797* (15), *H4964* (36), *H6028* (36), *H6495* (42), *H6642* (44), *H6693* (26), *H6740* (40), *H6744* (42), *H6761* (43), *H6927* (42), *H7118* (45), *H7119* (45), *H7408* (42), *H7849* (43), *H8114* (45), *H8115* (16), *H8401* (18), *H8411* (36), *H8484* (36), *H8671* (20), *H8801* (42), *H9641* (44), *H9756* (16), *H9801* (43), *H10333* (16), *H10428* (16), *H10618* (16), *H11283* (45), *H11840* (52), *H13082* (16), *H14492* (15), *H14520* × *kewensis*, *H14771* (44), *H15036* (45), *H15310* (45), *H15468* (38), *H15521* (44). *Englemann s.n.* 14 July 1868 (12), *s.n.* (14). *Erlanson 424* (55). *Everett 9407* (13). *Eyerdam 64* (20), *139* (16).

Fairchild s.n. Aug 1924 (34). *Faris 179* (16), *291* (16), *418* (30), *488* (44). *Fée s.n.* (2). *Fendler 440* (15), *445* (15), *640* (35). *Fernald & Long 3913* (2), *6195* (2), *7425* (2), *9914* (2), *10246* (2), *10247* (2), *10248* (2), *11019* (2), *11817* (2), *12063* (2), *12064* (2), *12333* (2), *14322* (2), *14323* (2), *14817* (2). *Fernald & Wiegand 14703* (46). *Fernando 649* (33). *Ferris 377* (13), *615* (13), *5686* (23), *6308* (13). *Field & Hunt s.n.* (12). *Figueriras 998* (28), *1185* (17). *G. L. Fisher, 35500* (35). *H. L. Fisher 1281* (2), *Fishlock 443* (15). *Flint s.n.* Feb 1868 (35). *Fogg 14857* (12). *Forsstrom s.n.* (15), *s.n.* (27). *Forster s.n.* ann. 1857 (2), *s.n.* May 1832 (2), *s.n.* (2), *s.n.* ann. 1853 (12), *s.n.* ann. 1854 (12). *Fox & Beaman 4760* (12). *Frank s.n.* (2). *Fredholm 6190* (2). *Freer 1487* (12), *1543* (12). *Frémont s.n.* ann. 1845-7 (13). *French s.n.* 15 July 1873 (14). *Fretz s.n.* ann. 1880 (2), *s.n.* ann. 1881 (14). *Friesner 16776* (2), *17172* (2). *Fritchey s.n.* 4 Sept 1888 (2). *Fuertes 26* (19), *411* (43), *413* (16), *902* (26), *965b* (16), *973b* (19), *974b* (26), *982* (43), *1879* (43). *Fuller 1141* (2).

Galen 82 (2), *2328* (2). *Galeotti 209* (37), *212* (23), *213* (41). *Garber s.n.* 18 Aug 1868 (12). *Gattinger 404* (14), *2330* (14), *s.n.* Apr (2), *s.n.* June (2), *s.n.* July 1883 (2), *s.n.* (2), *s.n.* June 1883 (12), *s.n.* July 1884 (12), *s.n.* May (14), *s.n.* May 19 (14), *s.n.* Mar 1875 (14), *s.n.* May 1879 (14), *s.n.* May 1880 (14), *s.n.* (14). *Gaumer 33* (35), *327* (35), *1106* (39), *23983* (39), *24105* (39), *24340* (39), *24364* (33), *24403* (39), *24456* (39), *24457* (33), *s.n.* Aug 1886 (35). *Gentle 16* (15), *1522* (39), *1959* (35), *2755* (48), *2948* (22), *3131* (35), *3536* (48), *3604* (15). *Gentry 6824* (23). *Ghiesbreght 214* (23), *800* (3). *Gibbes s.n.* Sept 1850 (2), *s.n.* ann. 1857 (2), *s.n.* ann. 1885 (2), *s.n.* (2). *F. A. Gilbert, & Plymale 724* (12). *G. Gilbert, s.n.* June 1894 (12). *Gilly s.n.* 26 May 1939 (12). *Glassman 1896* (39), *1921* (50). *Glatfelter s.n.* 2 June 1892 (2), *s.n.* 19 May 1892 (14). *Gleason 2303* (14). *Godfrey & Tryon, Jr. 465* (2), *998* (2), *1025* (2), *1158* (2). *Goodman 5983* (14). *G. B. Grant 2500* (13), *5279* (13). *V. Grant 748* (50). *Gray s.n.* ann. 1846 (2), *s.n.* ann. 1846 (12), *s.n.* ann. 1866 (12), *s.n.* (12), *s.n.* ann. 185- (14), *s.n.* ann. 1867 (29), *s.n.* ann. 1869 (29). *Gray, Sargent, Redfield & Canby 11771* (12). *Green s.n.* 9 July 1860 (2). Greene *s.n.* May 1887 (12). *Greenman 204* (12), *454* (35), *3979* (14), *4332* (14). *Gregg 1056* (23), *1088* (23). *R. B. Griffith 1* (13). *R. E. Griffith 85* (2). *Griffiths 7700* (23). *Gurney s.n.* 18 Jan 1899 (35), *s.n.* 16 Feb 1900 (35). *Guttenberg s.n.* ann. 1879 (2), *s.n.* ann. 1878 & '80 (12).

M. E. H., s.n. May 1883 (2). *Hale s.n.* (2). *E. Hall 528* (1), *529* (1), *s.n.* (1), *s.n.* 20 May 1872 (2), *s.n.* June 1873 (2), *s.n.* 4 July 1872 (14). *H. M. Hall, 1682* (13), *s.n.* 23 Apr 1899 (13), *s.n.* 23 Apr 1900 (13), *s.n.* 24 Apr 1900 (13). *Hannibal s.n.* 7 Apr 1907 (13). *Harbison s.n.* ann. 1897 (12). *Hardgrave s.n.* Dec 1921 (15). *Hardin & Duncan 15361* (14). *Harger 7191* (2), *s.n.* 24 June 1887 (2). *Harger & W. A. S. s.n.* 24 June 1887 (2). *Harper 246* (2), *309* (2), *499* (2), *581* (2), *1223* (14). *Harris 6655* (34), *10655* (33), *11631* (33). *Hartweg 565* (4), *566* (49). *Harvey s.n.* ann. 1844 (2), *s.n.* ann. 1844 (12), *s.n.* (12). *Hasse 6798* (1), *s.n.* May 1886 (1), *s.n.* 1 May to 2-3 July 1886 (1). *Hatch & Wilson* 25 July 1936 (6). *Haught 4648* (22). *Hayes 146* (49), *294* (49), *620* (22), *781* (49), *s.n.* July-Nov 1860 (39). *Heim, Cailleux & Stresser-Péan s.n.* 11 July 1959 (3). *Heller 7882* (13), *10687* (13), *11195* (13), *14480* (13), *Heller & Brown 5042* (13). *Heller & Heller 861* (30). *Hennecart s.n.* 28 July 1827 (2), *s.n.* Apr 1827 (16). *Bro. Heriberto 247* (49). *Hermann 2648* (24). *Herre s.n.* June 1893 (2). *Hess 807* (43). *Heyde 342* (39), *396* (35). *Heyde & Lux JDS 3824* (39), *JDS 3825* (35), *JDS 6373* (50). *Hinton 3141* (54), *4310* (54), *5258* (57), *8467* (57), *11605* (23), *12623* (21), *13530* (54), *14569* (6), *15151* (53), *15816* (23), *16147* (34), *16167* (23), *s.n.* 7 Mar 1933 (21). Hitchcock *809* (14), *s.n.* June-July 1894 (2), *s.n.* June-July 1898 (2), *s.n.* Aug 1892 (14), *s.n.* 17 Dec 1890 (35), *s.n.* 24 Dec 1890 (35), *s.n.* (35). *Bro. Hivram s.n.* Oct 1912 (15), *s.n.* Oct *1913* (15), *s.n.* Mar 1914 (15). *Hjalmarson s.n.* ann. 1850 (15), *s.n.* ann. 1853 (50). *Hodge 3198* (15). *Hodge & Howard 4317* (28). *Hoffman s.n.* (22). *Hogg s.n.* Mar 1888 (35). *Holdridge 891* (16), *1104* (45). *Holman s.n.* 12 Apr 1933 (13). *Holton*

s.n. July 1845 (2), *s.n.* 16 May 1854 (15). *Hood s.n.* 14 Apr 1911 (2). *Hoover 2769* (13). *Hornbeck s.n.* (15). *Horr & McGregor E481* (14). *House 1008* (2), *4253* (12), *4425* (12). *Howard 5959* (17), *12366* (16). *Howard, Briggs, Kamb, Lane & Ritland 74* (28), *430* (28). *Howard & Howard 8387* (16), *9185* (43). *Howell 8502* (21), *20864* (13). *Huger s.n.* Aug *1902* (2). *Hunnewell 9751* (2), *9953* (12), *10739* (2), *11682* (2), *12023* (2), *17475* (12), *17737* (2), *18825* (35), *18950* (12), *19333* (2). *Hunt s.n.* 27 Feb 1899 (13). *Hyams s.n.* July 1898 (2).

A. G. J. 79 (14). *Jack 4044* (33), *4709* (24), *5059* (24), *5509* (24), *8425* (35), *8633* (28). *Jamain s.n.* (15). *L. James 26* (14). *R. L. James 24* (2). *Jaramillo-Mejía & Fernández 715* (47). *O. E. Jennings 827* (12). *S. K. Jennings s.n.* ann. 1870 (2). *Jennison & Anderson s.n.* 14 May 1928 (12). *Jepson s.n.* 28 Apr 1893 (13). *Jicarda 41* (45), *1131* (16), *1281* (42). *Jimenez 1985* (15), *2006* (30), *2671* (33), *2716* (28), 2736 (15), 3743 (19). *Johnson 2328* (2). *I. M. Johnston 726* (55), *1253* (55), *1316* (55). *J. R. Johnston 923* (43), *s.n.* 6 June 1903 (35). *Jones 214* (13).

Kappler 1604 (15). *Kearney 41* (2), *84* (2), *105* (12), *286* (12), *516* (12), *591* (12), *878* (2), *1075* (2), *1242* (2), *s.n.* 28 May 1894 (2), *s.n.* 23 May 1897 (2), *s.n.* 10 Apr 1893 (12), *s.n.* ann. 1893, (12). *Kellerman 5870* (50), *6590* (35), *6592* (35), *7074* (50), *7826* (50), *8094* (35). *A. Kellogg 851* (13), *s.n.* (13). *A. Kellogg & Harford 851* (13), *857* (13). *J. H. Kellogg 860* (2), *s.n.* 20 May 1899 (2). *Kelley s.n.* 27 May 1905 (13). *Kenoyer 342* (22). *Key s.n.* May 1893 (15). *King s.n.* ann. 1894 (13), *s.n.* ann. 1897 (13). *Kittredge s.n.* 5 June 1940 (12). *Klug 4168* (34). *Koenig s.n.* 1 June 1899 (12). *Koleman 1065* (12). *Kotschy s.n.* (12).

Lamb 386 (23), *462* (23). *Lane s.n.* Aug 1921 (14). *Langlassé 199* (21). *Lankester 1305* (50), *1313* (39). *Leavenworth s.n.* ann. 1839 (2), *s.n.* (2), *s.n.* (14). *Leewis s.n.* (13). *Leggett s.n.* 6 July 1864 (2), *s.n.* 7 July 1865 (2), *s.n.* July 1865 (2), *s.n.* ann. 1867 (2), *s.n.* ann. 1868 (2), *s.n.* 12 Aug 1868 (2), *s.n.* 6 July 1869 (2), *s.n.* June 1868 (12), *s.n.* ann. 1868 (12), *s.n.* ann. 1868 (14). *Lehmann 1702* (50). *Lemaire s.n.* (2). *Lemmon s.n.* May 1883 (13). Leningrad Herbarium *s.n.* (2). *Bro. León 462* (28), *692* (24), *1464* (24), *3641* (43), 3652 (43), *4832* (24), *6495* (24), 6853 (37), *7164* (37), *11409* (33), *12041* (18), *14930* (33), *15808* (28), *16265* (28), *17268* (18), *22377* (43). *Bro. León & Cazañas 5969* (24). *Bro. León & Roca 8176* (28). *Bro. León & Ruiz 11405* (43). *Bro. León & Sauchez 8462* (24). *Bro. León & Victorin 20270* (17), *21010* (43), *22300* (43). *J. León* 367 (33), *687* (56). *E. C. Leonard 3061* (16), *4847* (45), *4847a* (45), *4869* (16), *4987* (44), *5244* (20), *7106* (16), *7209* (18), 7230 (18), *7281* (44), 7393 (16), *7413* (18), 7686 (16), 7757 (18), *8046* (18), *9037* (18), *9780* (18), *9781* (16), *9837* (16), *9956* (16), *10029* (18), *s.n.* 24-25 May 1920 (45). *Leonard & Leonard 11225* (16), *11390* (16), *12440* (16), *12558* (18), *12589* (16), *12671* (16), *13059* (16), *13115* (16), *13310* (16), *13767* (18), *13831* (16), *14658* (16), *14977* (18), *15008* (18), *15019* (18), *15095* (16), *15275* (16), *15558* (16), *15746* (45). *Le Roy s.n.* ann. 1867 (2), *s.n.* 17 Feb 1869 (13). *Letterman s.n.* June 1894 (2), *s.n.* May 1898 (2), *s.n.* 15 May 1912 (2), *s.n.* 27 Aug 1878 (14), *s.n.* 30 June 1879 (14), *s.n.* ann. 188- (14), *s.n.* 20 June 1880 (14), *s.n.* ann. 1882 (14), *s.n.* June 1894 (14), *s.n.* Apr 1900 (14), *s.n.* (14). *Levy 448* (35), *1129* (39). *L'Herminier s.n.* May 1843 (15). *Leibmann 99* (41), *409* (41). *Lighthipe s.n.* 20 June & 13 July 1891 (2), *s.n.* 25 July 1893 (2). *Linden 49* (34), *310* (34), *s.n.* ann. *1840* (34). *Lindheimer 299* (1). *Lindsay 488* (8). *Lix* 633 (2), *660* (12). *B. Long 17560* (2), *23619* (2), *41859* (2). *L. E. Long 149* (15). *Lopez 1588* (30). *Loring s.n.* 20 Oct 1899 (12), *s.n.* 12 June 1906 (12), *s.n.* Sept 1906 (12). *Lowrie s.n.* June 1874 (12). *Luna 474* (24), *500* (24). *Lundell 878* (39), *964* (39), *2318* (33). *Lundell & Lundell* 7257 (10), *8437* (14).

Macbride 2763 (39). *Mac Elwee 744* (2). *Mackenzie* 730 (2), *1119* (2), *1437* (2), *1690* (2), *7064* (2), 7443 (2). *Maltby* 6 (23), *143* (23). *Manning s.n.* June 1885 (14). *Marie-Victorin & Marie-Victorin 21501* (17). *Markens s.n.* (14). *Martínez-Calderón 74* (35). *Martius s.n.* ann. 1817 (15). *Mason 910* (13), *1697* (23), *1778* (23), 2683 (13), *2797* (13), *3717* (13), *4331* (13), *7995* (13). *Matuda 494* (35), *1755* (5), *2138* (39), *2234* (35), *16488* (22), *17132* (49), *17245* (49), *17628* (35). *Matz 2328* (2). *Maxon, Harvey & Valentine 7348* (33). *Maxon & Hay 3291* (35). *A. J. MC* (?) *s.n.* 31 May 1887 (12). *I. F. MC* (?) *s.n.* 26 Aug 1895 (33). *McCarthy s.n.* (2). *McClure s.n.* 2 Feb 1905 (15). *Mc Farland 60* (12), *4527* (12). *Mc Farland & Rogers 4665* (12). *H. E. Mc Minn 363* (13). *I. M. Mc Minn 1841* (2), *s.n.* (2). *Mc Murphy s.n.* 1 Apr 1914 (13). *Mc Vaugh 8470* (1). *Meislahn 122* (2). *Meredith s.n.* 11 June 1920 (2). *Merrill 243* (14), *1053* (14). *Merrill & Hagan 1053* (14). *Mertz 2328* (2), *2329* (12). *Mexia 1057* (23), *1069* (23), *1666a* (4),

2772 (4), *8790* (54). *Meyer s.n.* Apr 1929 (13). *Michaux s.n.* (1), *s.n.* (2), *s.n.* (12). *Michener & Bioletti 115* (13), *s.n.* ann. 1892 (13). *E. R. Miller s.n.* 18 Sept 1897 (2). *G. S. Miller Jr. 219* (45). *Milligan s.n.* May 1896 (1), *s.n.* June 1886 (2), *s.n.* Apr. (14). *Millspaugh 182* (12), 1958 (35). Charles Mohr Herbarium *s.n.* (2), *s.n.* 14 June 1883 (14), *s.n.* (14). *Moldenke 709* (39), *2431* (12), *4766* (46), *5449* (33), *5551* (39). *Molina 68* (39), *794* (39), *1341* (4), *1419* (50), *3076* (39), *10691* (11). *Monnet 691* (13). *Montes & Salazar 132* (23), *254* (23). *Mooney s.n.* ann. 1888 (2), *s.n.* ann. 1888 (12). *Moore 2332* (12). *Morris 1014* (12), *Morton & Acuña 2930* (17). *Moseley s.n.* 1 Aug 1897 (2). *Mosier s.n.* Jan 1930 (39). *Munroe s.n.* ann. *1857* (2).

Nash 950 (16), *952* (18), *1139* (2). *Nash & Taylor 1394* (16), *1451* (16). *Nee s.n.* (21). *Nelson 3746* (35), *4304* (23), *6981* (21). *Nelthrop 6* (35). *Nicolson s.n.* (15). *Nieuwland 63* (2). *Northrup & Northrup 568* (28). *Norton 327* (2), *s.n.* 4 July 1900 (2).

Oberhalser s.n. Aug 1895 (12). *Oberly s.n.* 10 Aug *1878* (2). *Oersted 102* (50), *s.n.* (50). *Ohlendorf 9330* (12), *Orcutt 4560* (23). *Ortega 64* (23), *132* (23), *222* (23), *391* (23), *4011* (23), *5564* (23), *10773* (23). *Osborn 1377R* (14). *Otero 491* (30). *Oyster 2329* (14), *s.n.* June 1885 (14).

T. C. P. (?) *s.n.* ann. 1864 (14). *Padilla 27* (39), *113* (39). *Painter 1320* (2). *E. Palmer 67* (23), *351* (21), *1247* (23). *E. J. Palmer 1503* (2), *1986* (2), *2136* (14) *2136a* (14), *2422* (2), *4057* (14), 5733 (2), *5868* (14), 7389 (2), *7459* (2), *8058* (1), *8384* (1), *9970* (2), *9971* (2), *11828* (2), *12051* (1), *12102* (2), *13349* (2), *15610* (2), *16208* (14), *17466* (2), *19405* (14), *20658* (14), *21011* (14), *21077* (14), *22054* (14), *22281* (14), *22467* (14), *22777* (14), *22930* (14), *24972* (14), *26748* (14), *27002* (2), *32938* (14), *34704* (2), *35448* (14), *35504* (14), *39472* (2), *41685* (14), *44023* (14), *54523* (14), *s.n.* 8 Aug 1908 (2), *s.n.* 6 May 1906 (14). *W. Palmer s.n.* 8 July 1906 (2). *Parish 19078* (13). *Parker s.n.* 26 June 1862 (2). *Parks 2912* (14), *29482* (2), *40973* (2). *Patterson s.n.* Sept. 1877 (14). *Bro. Paul 374* (22), *517* (39), *587* (49). *Pavon s.n.* (50). *Payson s.n.* 30 May 1952 (2). Peabody Herbarium "*Gray 444*" (29). *Pennell s.n.* 28 July 1904 (46), *s.n.* ann. 1905 (46). *Percival s.n.* 5 Sept. *1887* (12). *Perdue & Blum s.n.* 28 Aug 1961 (30). *Pfeifer 1592* (39), *1658* (50), *1660* (50) *1684* (50), *1977* (33), *2451* (12), *2460* (12) *2462* (12), *s.n.* (14). *Phillips s.n.* 25 Mar 1928 (13). *Pittier 90* (22), *1737* (50), *2304* (55), *2326* (22), *4145* (35), *4431* (22), *4732* (22), *5008* (49) *5236* (22), *5463* (8), *5750* (8), *6872* (49), *7094* (22), *JDS 7604* (58), *8533* (35), *16020* (15), *16027* (22), *16039* (34), *16102* (56), *16129* (35), *16164* (22). *16430* (39). *Pittier, Tonduz & Tonduz 9286* (56). *Plank s.n.* 17 May 1892 (1), *s.n.* (2). *Plée s.n.* ann. 1821 (15), *s.n.* (15). *Plitt 835* (2), *1758* (46). *Poiret s.n.* (2), *s.n.* (15), *s.n.* (44). *Poiteau s.n.* (16), *s.n.* (18), *s.n.* (43). *Pollard 472* (2). *Pollard, Maxon & Maxon 242* (2), *337* (2). *Pollock 71* (12), *s.n.* 23 May 1895 (12), *s.n.* 25 May 1895 (12), *s.n.* 20 May 1897 (12), *s.n.* 22 May 1897 (12). *Porter s.n.* 21 Aug 1863 (12), *s.n.* June 1864 (14). *Price s.n.* June 1891 (2), *s.n.* 1 June 1897 (14), *s.n.* summer 1898 (14), *s.n.* 23 May 1900 (14). *Pring s.n.* 10 Mar 1908 (22), *s.n.* ann. 1903 (35). *Pringle 9273* (57), *13424* (4). *Prisc 178* (2). *Proctor 9572* (35). *Purpus 205* (39), *1916* (9), *4416* (9), *5508* (57), *6931* (22), *7290* (22), *7291* (22), *7394* (9), *7570* (9), *8170* (9), *9076* (39).

Quentin 13 (15), *67* (15). *Questel 582* (15), *859* (15), *s.n.* May 1940 (27), *s.n.* Sept. 29 (27). *Quiros 496* (22), *617* (33), *1427* (22).

Radford 5743 (2), *6109* (12). *Ratelle s.n.* 21 Oct 1891 (35). *Rattan 1877* (13). *Rau s.n.* ann. 1879 (14). *Raven 6419* (13). Rehder *s.n.* 24 Aug *1907* (12). *Renson 209* (35). *Rettig 460* (14). *Reuter s.n.* (12). *Reverchon 785* (14), *2131* (2), *2936* (1), *s.n.* 21 Oct 1900 (1), *s.n.* 8 Apr 1902 (1), *s.n.* 25 Apr 1903 (1), *s.n.* 7 May 1903 (1), *s.n.* Oct 4 (1), *s.n.* ann. 1879 (14). *Richard s.n.* (15), *s.n.* (16), *s.n.* (18), *s.n.* (27), *s.n.* (30), *s.n.* (31), *s.n.* (35), *s.n.* (44), *s.n.* (50). *Ricksecker 85* (50), *Ridgway 2904* (2), *s.n.* ann. 1873 (14). *Rimbach 37* (34). *Robbins 15* (13), *2766* (14). *Rock 899* (14). *J. V. Rodriguez 64* (50), *449* (50), *622* (39), *1138* (39), *1173* (39), *3410* (49). *L. Rodriguez 2467* (27), *3616* (35), *3868* (27), *3985* (27). *J. N. Rose 1459* (23), *1560* (23). *J. N. Rose, Fitch & Russell 3848* (44), *3964* (16). *J. N. Rose, Painter & J. S. Rose 8591* (57). *J. N. Rose, Standley & Russell 13908* (23), *14183* (23), *14509* (23). *L. S. Rose 42004* (13). *Rothrock 489* (35), *s.n.* (2), *s.n.* (14). *Roviroso 245* (34), *520* (41), *584* (34), *588* (34). *Rowlee s.n.* 16 Aug 1895 (46). *Rowntree s.n.* 23 Apr 1933 (13). *Roy 520* (46). *Rugel 184* (43), *345* (43), *346* (37), *s.n.* May 1843 (14), *s.n.* ann. 1842 (15). *Ruth 75* (2), *79* (12), *173* (12), *178* (12), *1112* (14), *1436* (12), *s.n.* May 1896 (2), *s.n.* May 1893 (12), *s.n.* June 1893 (12), *s.n.* May-July 1895 (12), *s.n.* July 1896 (12), *s.n.* July-Aug 1909 (12). *Rydberg & Imler* 353 (14).

F. L. S. (?) *9211* (15). *Sagra s.n.* (28), *s.n.* (37). *Salvoza 577* (33). *Santiago 1918* (23). *Sargent s.n.* 8 Mar 1894 (13) *s.n.* 10 Mar 1885 (35). *Schipp 75* (48), *384* (41), *956* (22), *S-125* (35), *S-173* (22), *S-407* (39), *S-415* (55), *S-477* (39). *Schlechtendahl s.n.* (22). *Schmidtt s.n.* ann. 1913 (13). *Schomburgk 679* (15), *s.n.* (15). *Schott 789* (39). *Schreiber 2375* (13). *Schuermeier s.n.* 8 July 1897 (2), *Seal s.n.* 30 June 1885 (2), *Sessé, Mocino, Castillo & Maldonado 4410* (43), *4411* (57), *4412* (53), *4415* (35), *4417* (37), *4422* (50), *4424* (57), *5317* (23), *s.n.* (57). *Shafer 43* (43), *111* (12), *177* (24), *634* (12), *635* (2), *841* (28), *1034* (28), *1060A* (28), *1149* (30), *1214* (28), *1449* (30), *1504* (12), *1536* (28), *3053* (17), *3573* (17), *3808* (15), *3817,* (17), *4307* (15), *7903* (18), *13444* (37). *Sharp, Clebsch & Clebsch 4864* (14), *Sharples 64* (2). *Sharsmith 4215* (13). *Shattuck 164* (22), *413* (55), *640* (32), *726* (22), *1076* (55). *Sheley s.n.* 8 July 1909 (1). *Shipman s.n.* June *1878* (12), *Shirley 1250* (14), *Short s.n.* (2), *s.n.* ann. 1850 (46). *Shreve 1646* (2), *Shriver 180* (12), *s.n.* Aug 1891 (2). *Sieber 271* (15), *Simms s.n.* 1 May 1896 (2). *Simpson s.n.* 7 June 1953. *Sindel 38* (13). *Sintenis 812b* (15), *2490* (43), *3056* (43), *s.n.* Dec 1886 (15). *Small s.n.* 11 June 1892 (2), *s.n.* 9-12 July 1895 (2), *s.n.* 28 May 1892 (12), *s.n.* 29 May 1892 (12). *Small & Carter 8767* (28). *Small, DeWinkeler & Mosier 11278* (2), *Small & Heller 434* (12), *s.n.* 16-17 June 1891 (12). *Small, Mosier & Matthaus s.n.* 17 May 1926 (39). *Small, Small & DeWinkeler s.n.* Dec 1921 (39). *A. Smith P2249* (50), *P2449* (50). *Herbert H. Smith 1636* (50). *Huron H. Smith 1705* (12). *H. H. Smith & G. W. Smith* 333 (15), *333a* (15). *J. D. Smith 1245* (30), *1649* (39), *2063* (35), *2064* (35), *2065* (35), *2080* (39),*s.n.* 9 Aug 1881 (12), *s.n.* 11 Aug 1881 (12). *L. B. Smith & Hodgdon 3927* (12). *L. B. Smith, Hodgdon, Cheadle, & Taylor 3134* (28). *L. B. Smith, Hodgdon, Gilbert & McCoy 3474* (2), *L. E. Smith s.n.* Mar 1913 (13). *R. J. Smith s.n.* June 1905 (2). *S. C. Smith & J. D. Smith 136294* (12). *Solés s.n.* 17 May 1925 (23). *Sorme 1462* (13). *Standley 123* (50), *274* (50), *824* (39), *1350* (39), *4787* (4), *5686* (12), *8368* (39), *8762* (39), *8786* (2), *9553* (2), *9734* (11), *9850* (11), *11319* (50), *12207* (50), *17950* (50), *18382* (35), *18462* (39), *19441* (50), *19490* (39), *19897* (58), *20036* (5), *20545* (35), *20821* (39), *20825* (50), *21262* (50), *21978* (39), *22313* (50), *22529* (50), *22596* (39), *22734* (4), *23197* (35), *25740* (8), *26246* (49), *26770* (49), *27029* (49), *27090* (39), *27469* (32), *27796* (49), *27856* (39), *27963* (49), *29504* (22), *29515* (8), *29796* (49), *29804* (39), *29906* (8), *29950* (8), *31093* (22), *31839* (39), *40866* (32), *41117* (22), *44944* (22), *53031* (15), *53255* (22), *53415* (22), *54281* (15), *54743* (22), *58982* (4), *60540* (50), *62058* (49), *63140* (4), *63715* (4), *64137* (39), *66672* (35), *68409* (22), *68811* (49), *68892* (35), *68993* (39), *70707* (39), *72229* (22), *72866* (5), *73672* (50), *74126* (50), *74342* (50), *74359* (39), *74436* (50), *74574* (50), *75186* (50), *75458* (39), *75891* (39), *75895* (50), *76290* (50), *78336* (39), *78395* (35), *78501* (39), *78724* (49), *78870* (5), *78921* (50), *78970* (5), *79269* (39), *79286* (49), *79599* (49), *87226* (49), *87299* (39), *87997* (35), *88495* (5), *88611* (35), *88710* (39), *89233* (39), *89351* (30), *89555* (39). *Standley & Chacón 5227* (50), *5422* (50), *5784* (39). *Standley & Padilla 2745* (50), *3028* (5), *3089* (50), *3217* (50), *3784* (50). *Standley & Valerio 46667* (50), *48755* (58). *Stason & Rously s.n.* 28 Feb 1926 (13). *Stearns s.n.* 30 June 1904 (13). *Steele 53* (12), *s.n.* Aug-Sept 1898 (12), *s.n.* 16 Aug 1898 (12). *Stehlé 427* (27), *561* (27), *711* (15), *1863* (15), *2873* (27). *Stehlé & Stehlé 5073* (15). *Stephenson s.n.* 17 Oct 1928 (14), *s.n.* 17 May *1929* (14). *Stern, Chambers, Dwyer & Ebinger 204* (32). *Stevens 2174* (14), *2454* (14), *2528* (14), *2773* (2). *Stevenson 2948* (15), *3570* (30). *Stewart s.n.* (2). *Steyermark 4932* (2), *4973* (2), *5006* (2), *5099* (2), *5178* (2), *5314* (2), *5307* (14), *5826* (2), *6312* (2), *6457* (14), *6469* (2), *6839* (14), *7166* (2), *7434* (2), *7574* (14), *9714* (2), *9774* (14), *9791* (14), *9979* (14), *10348* (14), *10574* (14), *10942* (2), *11207* (14), *11510* (14), *11584* (2), *11638* (2), *11743* (2), *11974* (2), *12121* (2), *12674* (2), *12933* (2), *14145* (2), *14306* (14), *14328* (2), *14542* (14), *14661* (14), *14681* (2), *15292* (2), *15542* (2), *15567* (2), *15708* (2), *19186* (14), *19250* (2), *19335* (2), *19427* (14), *19756* (2), *19839* (2), *19869* (14), *20453* (14), *21337* (2), *21474* (2), *22081* (2), *22564* (14), *22623* (14), *22683* (2), *22795* (2), *22950* (14), *23079* (14), *23381* (2), *23775* (2), *24219* (2), *24380* (14), *24777* (2), *24883* (14), *24953* (14), *25119* (14), *25122* (2), *25324* (14), *25513* (2), *25515* (14), *25600* (14), *25833* (2), *25990* (2), *26085* (2), *26210* (2), *26315* (2), *26435* (2), *26581* (2), *26839* (14), *26849* (2), *27007* (2), *27166* (14), *27172* (2), *27382* (2), *27490* (14), *27528* (14), *27545* (2), *27631* (2), *27645* (14), *27647* (2), *27690* (2), *27752* (14), *27780* (2), *27865* (14), *28405* (2), *28803* (2), *28954* (2), *28981* (14), *30091* (50), *30351* (50), *30758* (39), *31796* (49), *33319* (22), *33455* (5), *35232* (35), *37231* (35), *37308* (22), *37592* (5), *40040* (2), *40076* (2), *40080* (14), *40132* (14), *40167* (2), *41093* (2), *41094* (14), *41148* (2), *41325* (14), *41368* (2), *41513* (14), *41790* (31), *42136* (50), *42148* (39), *43329* (35), *44973* (5), *46521* (5),

47902 (5), *51269* (7), *52321* (5), *63588* (2), *63721* (14), *63808* (2), *64002* (2), *64120* (2), *64160* (12), *64511* (12), *64686* (2), *64746* (14), *64755* (2), *64800* (2), *64931* (2), *65151* (2), *65376* (2), *65450* (2), *65723* (2), *66001* (2), *66086* (2), *66323* (14), *66404* (14), *66510* (2), *66535* (2), *66591* (2), *66933* (2), *67987* (2), *68795* (14), *68918* (2), *69958* (2), *70503* (2), *71399* (2), *71685* (2), *72698* (14), *73350* (14), *73354* (2), *73665* (2), *74017* (2), *74239* (14), *74351* (2), *77924* (14), *s.n.* 13 July 1936 (14). *Steitz s.n.* 29 June 1897 (2). *Stone s.n.* ann. 1896 (13), *Stork 18* (22). *Stork, Eyerdam, Morrison & Horton 25406* (23). *Sudworth 85* (12), *s.n.* 9 Aug 1890 (12), *s.n.* 20 June 1891 (2). *Svenson 9450* (14). *Swartz s.n.* (15), *s.n.* (16), *s.n.* (18), *s.n.* (27), *s.n.* (34), *s.n.* (35), *s.n.* (43). *Swink* 3333 (12).

Taylor s.n. 9 June 1912 (13), *Tharp 74* (1), *896* (1), *s.n.* 14 Sept 1923 (1), *s.n.* 15 May 1942 (1). *Thompson s.n.* 22 June 1896 (2), *Thorne 4109* (2). *Thurber 453* (13), *s.n.* (2). *Thurow 20* (1). *Tonduz 4100* (22), *8744* (35), *11548* (22), *13175* (56), *17878* (22), *17879* (56). *Tonduz & Pittier 9286* (56), *11549* (58). *Topping s.n.* 18 Oct 1896 (2), *Torrey Herbarium s.n.* (1), *s.n.* (2). *Torrey & Gray s.n.* (2). *Tosh 1161* (12). *Townsend s.n. Aug 1887* (35), *Tracy 1561* (13), *Trelease & Trelease 140/04* (23). *True 268* (2), *Tryon Jr. 2729* (2), *Tucker 688* (35). *Tuerckheim 2575* (45), *3072* (43), *JDS 5436* (35), *JDS 7768* (22), *JDS 7956* (5), *JDS 8452* (6), *JDS 8573* (35), *11395* (5), *11869* (35).

Underwood 44 (35). *Uribe-Uribe 2642* (47).

Vaillant s.n. (15), *s.n.* (16). *Valerio 35* (22), *895* (39), *961* (22). *Valeur 242* (33). *Van Sickle s.n.* 14 July 1893 (2), *s.n.* Aug 1894 (2). *Vargas s.n.* ann. 1829 (27). *Vasey s.n.* ann. 1878 (12), *s.n.* ann. 1870's (13), *s.n.* ann. 1875 (13), *s.n.* ann. 1876 (13), *s.n.* (14). *Virlet & Aoust s.n.* ann. 1871 (57). *Von Roszynski 184* (33).

C. F. W. (?) *s.n.* 10 Nov 1896 (30). *Waby 128* (15). *Walcott 2586* (15). *E. H. Walker 1474* (12), *F. Walker 19* (50), *Wall 2* (35), *Walsingham s.n.* ann. 1935 (24). *Ward s.n.* 24 June 1877 (2), *s.n.* 6 July 1884 (2). *Warner s.n.* May 25 (1). *Warscewicz 252* (47). *Watson 378* (35). *Weaver 542* (33), *Wedel 791* (34), *1002* (58), *1200* (34), *1201* (58), *1228* (22), *1247* (58), *1267* (22), *1404* (15), *1499* (58), *1556* (34), *1812* (15), *1841* (58), *2046* (34), *2903* (34). *Weil s.n.* Oct 1904 (2), *s.n.* June 1906 (2), *Weiss s.n.* 6 June 1923 (46), *Wercemont s.n.* (2), *Wetmore & Abbe 1* (32), *1A* (32). *Wetmore & Woodworth 77* (55). *Whalen & Jack s.n.* 8 Mar 1946 (13). *H. E. Wheeler 57* (14), *W. M. Wheeler s.n.* summer 1924 (14). *Whitehouse 658* (1), *15523* (14). *Wied-Neuwied s.n.* (2). *Wiegand s.n.* 16 June 1931 (12). *Wiegand & Manning 1086* (14). *Wiegand & Wiegand 411,* (1). *Wiggins 1378* (13). *Wight 104* (35). *Wilkes 1320* (13), *s.n.* ann. 1838-42 (13). *Wilkinson s.n.* (2). *L. Williams 9099* (48). *L. O. Williams & Molina 10449* (50), *10506* (50), *11156* (39), *11893* (50), *12066* (4), *14468* (35). *L. O. Williams & R. P. Williams 18811* (35). *R. S. Williams 204* (49), *527* (32), *548* (55). *C. H. Williamson s.n. May 1903* (2), *C. S. Williamson s.n.* Aug (12), *s.n.* June (46). *Wilson T-18* (14). *Wilsor 278* (22), *s.n.* 14 Aug 1915 (2). *Wolf 1741* (13), *8328* (13). *Wood s.n.* 25 July 1883 (2). *C. E. Wood, Jr. 3287* (12), *3614* (12), *6370* (2). *Woodson, Allen & Seibert 1739* (55). *Wright 463* (28), *2611* (24), *2612* (25), *2613* (34), *2614* (15), *2615* (37), *2616* (17), *2617* (42), 3665 (28), 3666 (43), *s.n.* (2), *s.n.* ann. 1859-60 (15), *s.n.* ann. *1860-4* (29), *s.n.* ann. 1853-56 (35), *s.n.* ann. *1853-56* (50). *C. Wright, Parry & Brummel s.n.* Jan-March, 1871 (44). *W. G. Wright 1281* (23).

Yates 3675 (13), *3850* (13). *Yuncker 4502* (35), *17944* (35), *18343* (33). *Yuncker, Koepper, Koepper & Wagner 8211* (34), *8466* (35), *8600* (39). *Yuncker & Welch 10854* (2).

Zetek 3618 (55).

INDEX OF LATIN NAMES

New taxa are in **boldface** type, all other taxa are in roman type; numbers in **boldface** type refer to descriptions, numbers in roman type refer to synonyms, numbers with dagger (†) refer to names incidentally mentioned.

Ambuya 122; labiosa 122†, 156

Aristolochia **122,** 115-194; anguicida 177, 187†; appendiculata 144; arborea 132†, **134,** 187†; arborescens 186†; argyroneura 174; arkansaw 140; asclepiadifolia **138,** 187†; aurantiaca 161; barbata 154; bilabiata 116†, 122†, **171,** 187†; bilobata 116†, **145,** 187†; biflora 166; brachyura 172; brasiliensis 156, *β* macrophylla 156, *γ* pariflora 156; **bullata 134,** 187†; calceiformis 171; californica **141,** 142†; 187†; **carterae 178,** 187†; caudata 144, **172,** 187†; chapmaniana **182,** 187†; chasmema **168,** 187†; clavidenia **152,** 187†; clematitis 174, 187†; clementis 146; clypeata 159; conduplicata 171; constricta **185,** 187†; convolvulacea 130; cordiflora 164; coriacea 142; costaricensis 149, 150†; cubensis 186†; cyclochilia 155; cymbifera 158†; dammeriana 186†; dictyantha 154, *β* schomburgkii 154; dodecandra 128; durior 186†; ehrenbergiana **173,** 187†; ekmanii **164,** 187†; elegans 118†, var. hassleriana 160; elliptica 165; inflata 187†; esoterica **159,** 187†; eurystoma 154; ferruginea 149; foetens 164; frutescens 140; fuertesii **153,** 187†; galeata 156; galeottii 151; geminiflora 166; gibbosa 176; gigantea 116†, **159,** 164, 187†; gigas 164; glandulosa **152,** 187†; glossa **180,** 187†; grandiflora 116†, 121†, 140, **157,** 164, 186†, 187†; haitiensis **148,** 187†; hassleriana 160; hastata 128, haughtiana 149; hirsuta 142; hitchcockii 142; inflata **176,** 186†; labiata 121†, **156,** 157†, 158†, 187†; labiosa 156; leptosticta **147,** 187†; leuconeura 186†; lindeniana 116†, **146,** 187†, var. plagiophylla 146; linearifolia **170,** 187†; littoralis 118†, **160,** 187†; loriflora 177; longifolia 186†; macradenia 152; macrophylla 116†, 121†, **140,** 141†, 143, 186†, 187†; macrota 144; macroura 144; malacophylla 132, 187†; martiniana 162; maxima 116†, **166,** 187†, *α* maxima 166, *β* geminiflora 166, *γ* augustifolia 166; mexiae 132; mexicana 166, 177; montana **179,** 187†; moschata 161; mycteria **181,** 187†; nashii 130; oblongata 171, 186†; oblongifolia 166; obtusata 154; obtusifolia 185; odoratissima **161,** 176, 187†, var. pandurata 162, *β* grandiflora 161; officinalis 128; orbicularis **185,** 187†; orinthocephala 156; ottonis 161; ovalifolia **169,** 187†; panamensis 116†, **136,** 187†; pandurata 161, 162; **paracleta 135,** 187†; pardina 151; passifloraefolia 116†, 119†, **155,** 187†; pavoniana 177; peltata 116†, **146,** 187†, var. poitaei 147; pentandra 116†; picta 161; pilosa **149,** 151†, 187†; podocarpa 186†; polyrrhizos 128; pubescens 186†; punctata 172, 186†; reniformis 146; reticulata **128,** 166, 187†; rhizantha **138,** 187†; rimbachii 162; ringens 156, **157,** 158†, 187†; rotunda 122†; rugosa **154,** 187†; rumicifolia 154; sagittata 128; salvadorensis 134; samanensis **166,** 187†; 1. scandens 161, 2. scandens 164, 3. scandens 144; schippii **175,** 187†; securidata 185; sericea 132; serpentaria 116†, 119† 120†, 122†, **128,** 186†, 187†, var. *β* 128, var. *γ* 128, *β* bartonii 130, *δ* hastata 130, *γ* laxa 130, var. nashii 130; sipho 122†, 140; spathulata 155; stenophylla 170; steyermarkii 134; surinamensis 144; sylvicola 159; taliscana **151,** 187†; tapetotricha 144; tentaculata **149,** 187†; thwaitesii **139,** 187†; tigrina 116†, **165,** 187†; tomentosa 121†, 141†, **142,** 187†; tonduzii **183,** 187; torta 176; tricaudata 132, 187†; trichostoma 155; trifida 144; triloba 144; trilobata 116†, **144,** 187†; tripteris 142; uhdeana 187†; veraguensis 116†, **174,** 186†, 187†

Cardiolochia 122

Dasyphonion 122; tomentosum 122†, 142

Diglosselis 122; trinervis 122†, 171

Dictyanthes 122; labiosa 122†

Endodeca 122; bartonii 128; dodecandra 130; hastata 122†; 128; polyrrhizos 130; serpentaria 128

Einomeia 122; bracteata 122†

Guaco 122; mexicana 122†

Hexaplectris 122; bicolor 122†

Hocquartia 122; macrophylla 122†, 140, tomentosa 142

Howardia 122; anguicida 177; barbata 154; benthamii 176; bilabiata 171; bilobata 145; costaricensis 149; caudata 172; ehrenbergiana 173; galeata 156; geminiflora 166; gigantea 159, 164; grandiflora 164; hoffmannii 166; inflata 176; macroura 144; maxima 166; obtusata 154; pandurata 161; peltata 146; pilosa 149; reniformis 146; ringens 122†, 157; schomburgkii 154; surinamensis 144; trilobata 144; veraguensis 174; warscewiczii 161;

Isiphia 122; glabra 122†, 140; tomentosa 142, 143

Isotrema 122; californa 141; durius 140; sipho 122, 140; tomentosum 142

Niphus 122

Pistolochia serpentaria 128
Plagistra 122; cretica 122†
Psophiza 122; undulata 122†, 128
Pteriphis 122; tripteris 122†
Siphidia 122
Siphisia 122; glabra 122†, 140; reticulata 128; sipho 140; tomentosa 142
Tropexa 122; biloba 122†, 145

THE GENUS ERYTHRONIUM (LILIACEAE) IN KANSAS[1]

BY KENNETH R. ROBERTSON[2]
Department of Botany, University of Kansas, Lawrence

ABSTRACT

Three species of *Erythronium* are recognized in Kansas, *E. rostratum* Wolf, *E. albidum* Nutt. and *E. mesochoreum* Knerr. *Erythronium rostatum* has erroneously been considered *E. americanum* Ker and both this species and *E. propullans* Gray are excluded from the state flora. *Erythronium mesochoreum* is recognized as distinct from *E. albidum* based on differences in chromosome number, the first diploid and the second tetraploid, and by different tendencies in vegetative reproduction, leaf morphology, perianth and fruiting characters as well as in habitat.

The genus *Erythronium* (*Liliaceae*) consists of one Eurasian, one Japanese, 4-6 eastern North American, and 17-24 western North American species. Five species are reported from Kansas, but the yellow-flowered *Erythronium* found in southeastern Kansas and adjacent Missouri had not been positively identified, the delimitation of white-flowered taxa was not clear, and several doubtful records for the state existed. This study was undertaken to resolve these questions.

YELLOW-FLOWERED SPECIES

The first eastern American species of a yellow-flowered *Erythronium* described was *E. americanum* by Ker (1808). Wolf (1941) described *E. harperi* and *E. rostratum,* though Parks & Hardin (1963) reduced *E. harperi* to *E. americanum* subsp. *harperi.*

Parks & Hardin examined specimens of *Franklin & McGregor E316* (NCSC) and *McGregor 15225* (US) and tentatively (without fruit) identified these specimens collected in Cherokee Co as *E. rostratum.* My own collections from this area *(93, 96, 121, 136, 149)* also are *E. rostratum.* Mature fruit was not seen; little or no fruit was apparently set in the colonies examined. In most flowers, the ovary withered soon after the tepals dropped; however, on some plants the ovary enlarged somewhat though the ovules within did not. These immature capsules were ellipsoidal with a prominent beak and were held erect. The specimens resembled those collected at the type locality by *Harper* 3832 (KSC) and an isolectotype *Morgan s.n.* (US 1786963).

Steyermark (1963) concluded that the yellow-flowered *Erythronium* found in southwestern, south central, and scattered southeastern and east central counties

[1] Rewritten portion of a thesis submitted to the Department of Botany and the Faculty of the Graduate School of the University of Kansas in partial fulfillment of the requirements for the degree Master of Arts.

[2] I wish to thank the curators of the herbaria at KANU, KSC, MO and US for the study of relevant specimens.

Present address, Department of Botany, Washington University, and the Missouri Botanical Garden, St. Louis.

ANN. MISSOURI BOT. GARD. **53**(2): 197-204, 1966.

of Missouri is *E. americanum* f. *americanum*. However, one of my collections from southwestern Missouri, in Christian Co, proved to be *E. rostratum* as did the relevant specimens at MO, i.e. those from southwestern Missouri, northwestern Arkansas, eastern Oklahoma and southeastern Kansas, while those from south-central and east-central Missouri and adjacent Illinois were *E. americanum* subsp. *americanum*. Apparently, Steyermark failed to distinguish the two species.

The chromosome number for *E. rostratum* was found to be $2n = 24$ (Appendix 1) confirming the report by Parks & Hardin (1963). All chromosomes have sub-terminal centromeres. The majority of species of *Erythronium* including the diploids *E. umbilicatum* Parks & Hardin, *E. grandiflorum* var. *pallidum* St. John, *E. revolutum* Smith, *E. montanum* S. Wats., *E. hendersonii* S. Wats., *E. oregonum* Appl., *E. dens-canis* L., *E. californicum* Purdy and the tetraploids *E. americanum* Ker and *E. americanum* subsp. *harperi* (Wolf) Parks & Hardin (Darlington & Wylie, 1955) have a basic number of $x = 12$ and all have substerminal centromeres.

White-Flowered Species

Nuttall (1818) described the eastern white-flowered *Erythronium* as *E. albidum*, distinguished by its mottled leaves, recurved tepals, the production of long horizontal stolons on immature forms, and its habitat in dense woods. Burgess (1877) and Panton (1877) independently reported from Iowa and Kansas, respectively, a white *Erythronium* differing from *E. albidum* by its narrower leaves which were unmottled, the tepals not recurved, and found in prairies rather than in woods. Neither worker named the form. It was validated by Knerr (1891a) from material collected in Atchison Co, Kansas who named it *E. messachoreum*. Later, Knerr (1891b) altered the spelling to *E. mesochoreum*. In his original paper, Knerr stated that the name meant Midland *Erythronium;* thus "mid-" would come from the Greek "mesos" which is prefixed "meso-" and so the spelling in the second paper is a correction for an orthographic error. Meads (1893) studied specimens of *E. albidum* from Michigan and *E. mesochoreum* obtained from Knerr. She suggested that the latter be considered as a variety of *E. albidum* but did not formally propose this reduction. Rickett (1937) found the separation of *E. albidum* and *E. mesochoreum* difficult near Columbia, Missouri and concluded that *E. mesochoreum* was an ecotype of *E. albidum* and proposed *E. albidum* var. *mesochoreum* (Knerr) Rickett. In his unpublished thesis using anatomical, morphological, and biosystematical methods, Ireland (1957) concluded that *E. mesochoreum* be relegated to subspecific status under *E. albidum*. However, he observed that when both taxa were planted in a common experimental garden they remained distinct.

Sterns (1888) described *E. albidum* var. *coloratum* based on material collected in McLennan Co, Texas in shaded woods near streams with white tepals more or less suffused with rose purple varying to bright red and leaves more strongly mottled with green and brown than in the typical variety. Shinners (1958) considered this variety synonymous with *E. albidum* var. *mesochoreum* and described it as having fewer stolons, either vertical or short and horizontal, colony composed predominantly of flowering plants with few sterile individuals, tepals lavender to

white, and found in open woods, thickets, and ravines bordering prairies; moreover his illustration shows a nonreflexed perianth and unmottled leaves. Steyermark (1963) did not agree with Shinners and stated that Sterns description seemed to apply more to a color variant of *E. albidum* rather than to *E. albidum* var. *mesochoreum*. I agree with Steyermark for the description given by Shinners of *E. albidum* var. *coloratum* is quite different from the original of Sterns while resembling that of *E. albidum* var. *mesochoreum*. I have examined specimens which were definitely *E. albidum* var. *mesochoreum* from near Ft. Worth and it seems likely that Shinners was referring to this taxon in his description of *E. albidum* var. *coloratum*.

Leaf morphology.

To determine the value of leaf size in separating *E. albidum* and *E. mesochoreum*, measurements of herbarium specimens were used. The first (outer) leaf of flowering plants was measured for length from the point at which it and the second leaf diverge and, for width, one centimeter below the leaf apex. The latter does not represent the widest point of the leaf and is not comparable to figures obtained by Knerr (1891a), Meads (1893) and Ireland (1957). Thirty-four specimens of *E. albidum* examined had an average length of 13.4 cm (8.0-22.0 cm), and an average width of 1.2 cm (0.6-2.0 cm). Sixty-four specimens of *E. mesochoreum* had an average length of 8.3 cm (5.0-13.6 cm), and an average width of 0.7 cm (0.2-1.2 cm). A leaf index was compiled using the length divided by the width as measured above and for *E. albidum* the average index was 11.4 (6.5-21.5) while for *E. mesochoreum* the average index was 12.9 (5.7-34.9). These show that although leaves of the latter species tend to be smaller, the proportion of length to width varies more within a species than between them.

Leaf width was measured 1 cm below the leaf tip so that an index could be compiled to measure the amount of pointedness at the tip. The index was made by dividing the width by 1 cm. The average index for *E. albidum* was 1.2 (mean 1.2, range 0.6-2.0), whereas *E. mesochoreum* had an average index of 0.6 (mean 0.6, range 0.2-1.2). This indicates that the leaves of the latter species are more gradually tapered toward the tip while those of the former are more abruptly attenuated.

Leaf mottling is a useful field character as the leaves of *E. albidum* are typically mottled while those of *E. mesochoreum* are not mottled. However, some leaves of *E. albidum* were seen with little mottling and two colonies of *E. mesochoreum* were found distinctly mottled. Also, as the season progresses, the purple pigment causing mottling disappears leaving splotches of light green and when specimens of *E. albidum* are dried, the mottling usually fades.

Leaf folding is also a valuable field character, for the leaves of *E. mesochoreum* are normally conduplicate while those of *E. albidum* are usually flat or half-folded at the most.

Floral morphology.

Reports by previous workers and personal observations indicate that there are no reliable floral differences between *E. albidum* and *E. mesochoreum*, except that the perianth in the former species is usually completely reflexed in full bloom while that of the latter is spreading or at most half-reflexed.

Fruit morphology.

Mature capsules of *E. albidum* average 1.6 cm (1.0-2.2) in length and 1.0 cm (0.7-1.3 cm) in width while those of *E. mesochoreum* average 1.4 cm (1.1-2.0) in length and 0.9 cm (0.6-1.7 cm) in width. These data indicate that fruit size is not a significant character as suggested by Knerr (1891a). However, the manner in which the mature capsule is held is indicative of the species. The fruit of *E. albidum* is held erect on a more or less erect peduncle, while the tip of the capsule of *E. mesochoreum* rests on the ground at the end of an arching peduncle. The capsule of both species is obovoid, that of *E. mesochoreum* having a distinct indentation at the tip while that of *E. albidum* is rounded, slightly apiculate, or with a slight indentation.

Vegetative reproduction.

The method of vegetative reproduction of sterile forms varies in the following ways:

	Stolons	*Droppers*	*Offsets*
E. mesochoreum	0	36 (13%)	245 (87%)
E. albidum	181 (56%)	5 (2%)	139 (42%).

The relevant features are the lack of stolons and the production of some droppers in *E. mesochoreum* with the formation of offsets as the major mode of vegetative reproduction. In *E. albidum* a significant number of sterile plants reproduced by offsets although the majority formed stolons. Flowering plants of both species regularly produce offsets. It was noted that these offsets are usually lateral in flowering plants, but often vertical in the sterile forms.

Chromosome numbers and morphology (Appendix 1).

The chromosome number of *E. mesochoreum* was found to be $2n = 22$ which confirms the reports of Ireland (1957) and Smith (1965). Eight of the chromosomes are metacentric or submetacentric while 14 are acrocentric. *Erythronium albidum* has $2n = 44$ as reported by Cooper (1939) and Ireland (1957). Sixteen chromosomes are metacentric or submetacentric while 28 are acrocentric. These species are the only members of the genus reported with a basic number of $x = 11$ and with metacentric or submetacentric chromosomes. No plant was found with an intermediate number of $2n = 33$ among 23 collections studied, including plants from a population where the two species were found together.

In summary, the two white-flowered species may be distinguished by a combination of the following characters:

mesochoreum	*albidum*
Leaves gradually attenuated	Leaves abruptly attenuated
Leaves not mottled	Leaves mottled
Leaves conduplicate	Leaves flat
Perianth spreading	Perianth reflexed
Fruit resting on ground	Fruit held erect
Sterile forms forming offsets and droppers	Sterile forms forming stolens and offsets
Chromosome number $2n = 22$	Chromosome number $2n = 44$
Prairies, pastures, dry woods.	Moist woods

Systematic Treatment

Three species of *Erythronium* recognized in Kansas.

a. Perianth segments yellow, auricles present; underside of leaves not glaucous .... 1. *E. rostratum*

aa. Perianth segments white, auricles absent; underside of leaves glaucous.

- b. Perianth segments reflexed in full bloom; leaves mottled; mature fruits held off ground; moist woods .... 2. *E. albidum*
- bb. Perianth segments spreading to at most half-reflexed in full bloom; leaves not mottled; mature fruits resting on ground; prairies, pastures, dry open woods .... 3. *E. mesochoreum*

1. Erythronium rostratum Wolf, Castanea **6**: 24, 1941.

Herb perennating by underground corm. *Leaves* 2 in flowering forms, 1 in immature forms, tapering into petioles which sheath the base of scape, strongly mottled on adaxial side at flowering with purplish-brown pigment, not glaucous. *Inflorescence* solitary at tip of scape. *Flowers* perfect with yellow tepals; outer tepals 3 with intense purplish-brown specks on abaxial side; inner tepals 3 with well developed auricles at base which clasp the opposite filaments; stamens 6, filaments opposite inner tepals slightly longer than those opposite outer tepals, anthers yellow, those opposite inner tepals maturing before those opposite outer tepals; stigma lobes swollen, short and erect, style persistent and forming prominent beak on capsule. *Fruit* ellipsoidal capsule with beak, held erect at maturity.

Lectotype: ALABAMA: Blount Co, Warnock Mt, *Morgan s.n.*, 4 Apr 1938, St. Bernard College Herb 4224 (SB, not seen), isolectotype (US).

Rich moist woods, especially along creek or river banks; northern & central Alabama, Tennessee, SE Kansas, SW & S central Missouri, E Oklahoma, NW Arkansas. Apparently not found in the lower Mississippi Valley. March-April.

KANSAS: Cherokee Co.

2. Erythronium albidum Nutt., Gen. N. Amer. Pl. 223, 1818.

Herb perennating by underground corm. *Leaves* 2 in flowering forms, 1 in immature forms, tapering into petioles which sheath the base of scape, elliptical-lanceolate to ovate-lanceolate, flat to half-folded, mottled on both sides with purplish-brown or light green, glaucous on both sides. *Inflorescence* solitary at tip of scape. *Flowers* perfect with white tepals, often tinged on abaxial side with pink, blue or lavender; outer tepals 3; inner tepals 3, without auricles, yellow spot present at base; perianth segments usually completely reflexed in full bloom; stamens 6, filaments opposite inner tepals slightly longer than those opposite outer tepals, anthers yellow, those opposite inner tepals maturing before those opposite outer tepals; stigmas trifid, lobes long and divergent, slender, style not persistent. *Fruit* obovate, held erect at maturity, rounded, slightly apiculate or slightly umbilicate at distal end.

Type: Unknown.

Moist dense woods, especially along slopes or banks overlooking creeks, lakes and rivers; Ontario and Minnesota south to Georgia, Kentucky, Missouri & Texas. March-early May.

kansas: Atchison, Bourbon, Brown, Cherokee, Cloud, Cowley, Crawford, Douglas, Geary, Jackson, Jefferson, Johnson, Labette, Leavenworth, Linn, Marshall, Miami, Montgomery, Neosho, Pottawatomie, Riley, Shawnee, Wabaunsee, Washington, Wilson & Wyandotte Counties.

3. Erythronium mesochoreum Knerr, Mid. College Monthly **2:** 5, 1891.

E. albidum Nutt. var. *mesochoreum* (Knerr) Rickett, Rhodora **39:** 105, 1937.

Herb perennating by underground corm. *Leaves* 2 in flowering forms, 1 in immature forms, tapering into petioles which sheath the base of scape, lanceolate to linear-lanceolate, conduplicate or occasionally half-folded, usually not mottled, glaucous on both sides. *Inflorescence* solitary at tipe of scape. *Flowers* perfect with white tepals, often tinged on abaxial side with blue or lavender; outer tepals 3; inner tepals 3, without auricles, yellow spot present at base, perianth segments spreading or at most half-reflexed in full bloom; stamens 6, the filaments opposite the inner tepals slightly longer than those opposite the outer tepals; anthers yellow, those opposite the inner tepals maturing before those opposite outer tepals; stigmas trifid, lobes long and divergent, slender, style not persistent on fruit; *Fruit* obovate, resting on ground at maturity, umbilicate at distal end.

Neotype: kansas: Atchison Co, Atchison, *Knerr s.n.*, 24 Apr 1891 (MO). No specimen was cited with the original description. This specimen selected as the neotype was collected by Knerr in the same locality where he found the new species and in the same year as the original description. The specimen matches the type description and possibly was from the material used by Knerr. In the Missouri Botanical Garden herbarium are two letters written by Knerr to Dr. W. Trelease. The first was written shortly before *E. mesochoreum* was published (Apr 24, 1891) and mentions specimens of both *E. albidum* and "*E.* ?" sent by Knerr to Trelease requesting the latter's aid in determining the material marked

"*E.* ?". In a second letter (May 13, 1891) Knerr stated that he had described the heretofore unknown material as *E. messachoreum* and enclosed a copy of the original description.

Prairies, pastures, and dry open woods; Iowa, Missouri, E Nebraska, E Kansas, Oklahoma, and Texas. March-April.

KANSAS: Allen, Anderson, Atchison, Bourbon, Butler, Chautauqua, Cherokee, Cloud, Crawford, Douglas, Franklin, Geary, Greenwood, Lyon, Morris, Neosho, Osage, Saline, Shawnee, Wabaunsee, Wilson & Woodson Counties.

Excluded Species

Knerr (1891a) reported *E. propullans* Gray from Kansas; no one has since collected it in the state. I have examined a specimen identified as the species from Davis Co (now part of Geary Co), *Panton s.n.*, 1879 (KCS) and although the sheet has only sterile forms each has stolons arising from the corms (characteristic of *E. albidum* in this region) instead of offshoots arising from about midway on the stem as is found in *E. propullans.* It seems unlikely that *E. propullans* occurs so far south from its normal range in Minnesota.

Smyth (1892) reported the Kansas distribution of *E. americanum* from Kansas City west to Manhattan and Junction City. I have examined *Smyth 1012* (Shawnee Co, 1887, KSC) and this specimen is *E. albidum;* very possibly Smyth confused the two species and I suspect his distribution for *E. americanum* is erroneous. No one has since collected the species in this area.

Literature Cited

Burgess, R. 1877. Additions to the Flora of Iowa. Bot Gaz. **2:** 115.

Cooper, D. C. 1937. Development of megagametophyte in *Erythronium albidum.* Bot. Gaz. **100:** 862-867.

Darlington, C. D. & A. P. Wylie. 1955. Chromosome atlas of flowering plants 2. George Allen & Unwin Ltd., London.

Ireland, R. R., Jr. 1957. Biosystematics of *Erythronium albidum* and *E. mesochoreum.* Unpublished Master of Arts thesis. University of Kansas.

Ker, J. B. 1808. *Erythronium americanum.* Bot. Mag. **28:** *t. 1113.*

Knerr, E. B. 1891a. *Erythronium messachoreum.* Mid. College Monthly **2:** 5.

————1891b. *Erythronium mesochoreum.* Trans. Kansas Acad. Sci. **13:** 20-21.

Meads, M. E. 1893. The range of variation of species of *Erythronium.* Bot. Gaz. **18:** 134-138.

Nuttall, T. 1818. Genera of North American Plants **1:** 223-224.

Panton, M. H. 1877. Some botanical notes from Kansas. Bot. Gaz. **2:** 123.

Parks, C. L. & J. W. Hardin. 1963. Yellow Erythroniums of the eastern United States. Brittonia **15:** 245-259.

Rickett, H. W. 1937. *Erythronium mesochoreum.* Rhodora **39:** 101-105.

Shinners, L. H. 1958. Spring flora of the Dallas-Fort Worth area Texas. Southern Methodist University, Dallas.

Smith, E. B. 1965. Chromosome numbers of Kansas flowering plants. Trans. Kansas Acad. Sci. **67:** 818-819.

Smyth, B. B. 1892. Checklist of the plants of Kansas. Topeka, Kansas.

Sterns, E. E. 1888. A new variety of *Erythronium.* Bull. Torrey Bot. Club **15:** 111-112.

Steyermark, J. A. 1963. Flora of Missouri. Iowa State University Press, Ames.

Wolf, W. 1941. *Erythronium,* a neglected genus in Alabama. Castanea **6:** 21-27.

Appendix 1

Cytological Materials, Techniques & Results

Stolon tips of *E. rostratum*, *E. albidum*, and young ovaries of *E. mesochoreum* were placed in a solution of 2% colchicine for 2 hours and fixed in modified Carnoy's fluid of 6 parts 95% ethanol, 2 parts propionic acid, and 2 parts chloroform. The growing tip of a stolon or a young ovule was dissected out and hydrolyzed in 10% HCl for 2-5 minutes, rinsed with fixative, teased apart in a drop of saturated propionocarmine and macerated gently.

Voucher specimens (all *Robertson*) are deposited at the University of Kansas (KANU) and many duplicates at the Missouri Botanical Garden (MO).

Erythronium rostratum Wolf: **2n = 24.** Kansas: Cherokee Co, 3 mi N of Baxter Springs, *121* (KANU, MO), *124* (KANU); 3.5 mi N of Galena, *127* (KANU, MO).

E. albidum Nutt.: **2n = 44.** Kansas: Cherokee Co, 3 mi N of Baxter Springs, *125* (KANU, MO); Douglas Co, 4 mi NW of Lawrence, *129* (KANU); Linn Co, Marais Des Cygne Waterfowl Refuge, *132, 146* (KANU, MO); Miami Co, SE part of Miami Co State Lake, *133* (KANU, MO); SW part of Miami Co State Lake, *134* (KANU, MO); Johnson Co, 4 mi E of Eudora, *135* (KANU, MO).

E. mesochoreum Knerr: **2n = 22.** Kansas: Allen Co, 2 mi N of Mildred, *118*; Anderson Co, 11 mi S of Garnett, *117*; Cherokee Co, 2.5 mi S of Galena, *122* (KANU, MO); 3 mi N of Baxter Springs, *126* (KANU); Crawford Co, N edge of Pittsburg, *148* (KANU, MO); Douglas Co, University of Kansas campus *115*; 4 mi NW of Lawrence, *128* (KANU); Neosho Co, 2 mi E of Neosho Co State Lake, *120* (KANU, MO); Osage Co, 1 mi E of Vassar, *130* (KANU, MO); Shawnee Co, 2 mi S of Forbes AFB, *131* (KANU, MO); 1.25 mi E of Dover, *143* (KANU, MO); Wabaunsee Co, 2 mi N & 0.5 mi W of Dover, *145* (KANU, MO). Missouri: Barton Co, 2 mi E of Mindenmines, *140* (KANU, MO).

TAXONOMIC STATUS OF CLAYTONIA ROSEA AND C. LANCEOLATA (PORTULACACEAE)[1]

BY DIANNE K. HALLECK [2,3] AND DELBERT WIENS
Department of Botany, University of Utah, Salt Lake City

ABSTRACT

Claytonia rosea Rydb., not currently recognized in the Rocky Mountains, is separable from *C. lanceolata* Pursh by gross morphological, karyological and ecological characters.

Claytonia rosea Rydb. is a species not currently recognized in the Rocky Mountains, and is usually synonymized under *C. lanceolata* Pursh (cf. Harrington, 1954; Weber, 1953). In Arizona *C. rosea* is accepted with the reservation that it may not be distinct from *C. lanceolata* (Kearney & Peebles, 1951). Davis (1966) in his study of the perennial species of *Claytonia* recognizes it as a variety of *C. lanceolata.*

Claytonia lanceolata was orginally described by Pursh (1814) from a collection of plants made by Meriwether Lewis on the Lewis and Clark Expedition (1806-07). The type locality is "on the Rocky Mountains," and the collection was made in June. The species is based on the following description: "foliis lanceolatis; caulinis ovatis sessilibus, racemo solitairo elongato, calycis brevibus obtusissimis, petalis cuneatis bifidis, radice tuberosa."

Rydberg (1904) described *C. rosea* on the basis of three collections from Colorado, the type locality La Veta. The species was mentioned as occurring between 5,000 and 7,000 ft, and characterized by the following description:

> "Scape about 1 dm high, slender, from a small corm 10-15 mm in diameter; basal leaves rare, long-petioled, blade 1-2 cm long, spatulate; stem leaves linear or narrowly linear-lanceolate, sessile, 2-5 cm long, 1 ribbed or faintly 3 ribbed, acute, rather fleshy; sepals rounded ovate, rounded at apex, about 5 mm long, half as long as the pink obovate petals; inflorescence 5-10 flowered, short, little exceeding the leaves, bractlets lanceolate; capsule shorter than sepals, seeds 2 mm long, black and very glossy."

GROSS MORPHOLOGY AND DISTRIBUTION

Part of the confusion which has existed in the application of the names *C. rosea* and *C. lanceolata* might be attributed to incompleteness of the original descriptions. Both species were based on seemingly atypical individuals. For example,

---

[1] This study was completed utilizing facilities of the Institute of Arctic and Alpine Research, University of Colorado, Boulder, Colorado. We acknowledge gratefully the assistance of the Institute, particularly its director, Dr. John Marr. We are indebted to Dr. R. K. Vickery, Jr. for critically reading the manuscript and to Sharon Harris who prepared the illustrations.

[2] Based on a dissertation submitted by the first author in partial fulfillment of the requirements for the degree of Master of Science at the University of Colorado.

[3] Present address: Havana High School, Havana, Illinois.

ANN. MISSOURI BOT. GARD. **53**(2): 205-212, 1966.

C. lanceolata is depicted in the illustration accompanying the orginal description with multiple basal leaves. Corms of *C. lanceolata* typically produce a basal rosette of leaves until they have reached a size sufficient for the production of flowering stems. Thereafter, flowering stems occur but basal leaves do not (Fig. 2). Conversely, flowering corms of *C. rosea* typically produce basal leaves, but they were noted as rare in the orginal description. Normally the number of basal leaves is two (Fig. 1), but this may be a function of the age of corms. From none (noted in a single population) to as many as ten basal leaves per corm have been observed in *C. rosea*.

Another inconsistency arising in current treatments concerns the petal apex (Fig. 1-2). *Claytonia lanceolata* generally has emarginate-retuse petals while those of *C. rosea* have rounded to acute apices. In the Rocky Mountains this character has been neglected, and the petals of *C. lanceolata* (s. l.) are described as "rounded to emarginate" (Harrington, 1954). In areas outside the range of *C. rosea*, such as the Pacific Coast and Idaho, the petals of *C. lanceolata* are usually described as emarginate to retuse (Abrams, 1944; Davis, 1952; Munz, 1959). Apparently, the morphological concept of *C. lanceolata* has become expanded to include *C. rosea* in areas where they occur together, but where *C. lanceolata* is the only species present the species description mentions only retuse or emarginate petal apices.

These two species are clearly distinguishable on a gross morphological basis. *Claytonia rosea* possesses rounded to acute petal apices, basal leaves ranging from linear to lanceolate and usually linear cauline leaves. *Claytonia lanceolata* is characterized by emarginate petals, absence of basal leaves, and elliptical to ovate cauline leaves. These characters, however, are subject to some variation. A population of *C. rosea* without basal leaves was discovered near Boulder, Colorado, but the petals are entire and cauline leaves are linear. In the Yellowstone area of Wyoming the cauline leaves of *C. lanceolata* are frequently more narrow than is typical. The petal is emarginate, however, and there are no basal leaves. Thus, a combination of any two of these characters, i.e. petal apices, cauline and basal leaves, will distinguish either taxon.

The geographical distribution of *C. rosea* is known to include the southern Rocky Mountains of south-central Wyoming and Colorado, western New Mexico and parts of northern Arizona. It may, however, also occur as far north as southern Montana. *Claytonia lanceolata* is more widely distributed, occurring from southern Canada to northern California on the Pacific Coast and to southern Colorado in the Rocky Mountains. The species are presently known to be geographically sympatric only in the southeastern Rocky Mountains, but even here they are usually altitudinally and ecologically isolated. Because *C. lanceolata* is widely distributed and highly variable, there appears to have been a tendency to overlook closely related geographically sympatric species, such as *C. rosea*.

Cytology

Methods—Young floral buds, root tips and leaves were fixed in a 3:1 solution of acid alcohol. Storage was in 70% ETOH. The aceto-carmine squash technique

Fig. 1-3. Illustrations of *Claytonia*. Fig. 1. *C. rosea*. Fig. 2. *C. lanceolata*. Fig. 3. Meiotic MI in *C. rosea*. × ca 1400.

was used to study microsporogenesis; for mitosis the Feulgen method was employed. Hydrolysis was in 1 N HCl at 60° C for 6 minutes. Somatic material was also killed and fixed directly in acid alcohol without pre-treatment.

We experienced significant difficulties obtaining floral buds undergoing meiosis in *C. lanceolata*. Apparently this species undergoes meiosis beneath deep snowbanks sometime during the winter or early spring (a topic discussed later). In contrast *C. rosea* is not associated with such melting snowbanks; consequently floral buds are easily obtainable shortly after emergence of the plants in early spring or late winter. Fortuitously, we discovered that corms of *C. lanceolata* maintained under refrigeration will produce immature plants from which some dividing PMC's were obtained. The chromosome numbers reported for *C. lanceolata* appeared reason-

ably clear, but the paucity of dividing cells in a given tissue generally prevented adequate verification of given numbers.

Voucher specimens for all phases of the study are deposited in the herbaria of the University of Colorado and the University of Utah.

Results and discussion—Cytologically, *C. rosea* appears to be a stable diploid species with a base number of $n=8$ (Table 1, Fig. 3). This number agrees with reports by Rothwell & Heiser (1951), Davis & Bowmer (1966) and Lewis (1966). With the exception of some PMC's which appeared to have trivalent and univalent formation, there was no significant deviation from the base number in the populations we examined. Because long polyploid-aneuploid series of chromosome numbers have been reported for the closely related *C. virginica* L. of the eastern United States (Rothwell, 1959, 1965; Lewis, 1962), several populations of *C. rosea* were sampled in depth for such variations in chromosome numbers; however, none were noted.

In *C. lanceolata*, however, we have not been able to resolve a definite base number. Our data (Table 1) show variation in both meiotic and mitotic chromosome numbers for *C. lanceolata*. This concurs with the results of Davis & Bowmer, who worked exclusively with meiotic material. However, where the two species are geographically sympatric, only polyploid numbers are presently known in *C. lanceolata*, but beyond the western range of *C. rosea* diplioid numbers ($n=8$) are also known in *C. lanceolata*: this likewise agrees with Davis & Bowmer, except that they report $n=8$ for *C. lanceolata* from Mesa Verde National Park, Colorado, where we found only diploid *C. rosea*.

An earlier report of $n=8$ in *C. lanceolata* (Wiens & Halleck, 1962) should be disregarded; the plants from which the chromosome numbers were determined actually were *C. rosea*.

The chromosome numbers of related species are of interest in order to determine a base number for the group. *Claytonia megarrhiza* (A. Gray) Parry is confined to the alpine areas of the Rocky Mountain system. Wiens & Halleck indicated a gametic number of between 16 and 18 for this species. Subsequent analysis of populations on Mt. Evans, Colorado, were $n=16$, which agrees with the report by Davis & Bowmer. Rothwell & Heiser (1951) reported $n=8$ in *C. caroliniana* Michx. and Johnson & Packer (1963) found $2n=16$ in the Alaskan species, *C. tuberosa* Pall. ex Willd. Sokolovskaya (in Cave, 1964) found $2n=30\text{-}32$ in *acutifolia* Pall. from the Kamchatkan peninsula. Rothwell (1959, 1965) indicates 8 as a modal number in his studies on *C. virginica*, although Lewis (1962) found $n=7$ as the mode in his observations of this species in Texas. In view of the recurrence of 8 in a number of diverse taxa, it appears at this time to emerge as a base number for the group.

Barriers to Gene Exchange

In the region of the Colorado Front Range, at least three factors appear to prevent hybridization between *C. rosea* and *C. lanceolata*. These include (1) ecological, (2) seasonal, and (3) chromosomal mechanisms.

Table 1. Chromosome numbers in *Claytonia rosea* and *C. lanceolata.*

C. rosea		*C. lanceolata*	
Chrom. no.	*Collection data*	*Chrom. no.*	*Collection data*
$n=8$	Flagstaff Mtn, Boulder Co, Colo.[a]	$n=22$	Nr St. Vrain Glacier, Boulder Co, Colo. *H 40*
$n=8$	Boulder Canyon, Boulder Co, Colo. *H 6.*	n=ca 27, ca 37, ca 38, ca 42, ca 45; $2n$ =ca 37, ca 52	Nr Pawnee Basin Campground, Grand Co, Colo. *H. 101.*
$n=8$	Left Hand Canyon, Boulder Co, Colo. *W 2831.*	$n=22$	Togwotee Pass, Jefferson Co, Wyo. *H 100.*
$n=8$	Magnolia Hill, Boulder Co, Colo.[b]	$2n=32$, 36	Nr Kamas, Summit Co, Utah. *D 5020.*
$n=8$	Lookout Mtn, Jefferson Co, Colo.[c]	$2n=24$	Pole Canyon, Utah Co, Utah. *D 5021.*
$n=8$	Mesa Verde Ntl Park, Colo.[d]	$2n=16$	North Bench, Salt Lake City, Salt Lake Co, Utah. *W 3037.*
$n=8$, $2n=16$	Nr Mogollon, Catron Co, N. Mex.[e]		
$2n=16$	Oak Creek Canyon, Coconino Co, Ariz. *CR 3.*		

[a] 24 counts representing 16 populations: *H 12, 20, 22, 25, 26, 30, 33, 35, 42-45, 48, 50 a-g, T-2.* Some possible univalent and trivalent formation.

[b] 5 counts. *H 55 a-e.*

[c] 5 counts. *H 51 a-c, H 52 a-b.*

[d] 4 counts. *H 60 a-b, H 61 a-b.*

[e] 6 counts. *W 3005.*

Ecological—Claytonia rosea is a species of the Rocky Mountain Montane Forest Association, occuring most frequently between the altitudes of 5,000 and 7,000 ft. Often it grows beneath stands of ponderosa pine (the dominant tree of this association) and around the small meadows typical of the region. *Claytonia rosea* usually appears several weeks after the snow melts from an area, and is one of the first spring flowers of the region.

However, *C. lanceolata* occurs in the regions where they are sympatric; the Rocky Mountain Subalpine Forest Association dominated by dense stands of spruce-fir, where it is most common between 10,000 and 11,000 ft and associated with melting snowbanks. Our observations suggest that in this environment vegetative and reproductive development occurs in this species during the winter or early spring while the plant is deeply covered with snow. Attempts to obtain young

plants which had not yet undergone meiosis by digging through snowbanks three to four feet deep proved unsuccessful. Active growth and reproductive development, including meiosis and flower formation, was observed in a few corms refrigerated at approximately 37° F through the winter. The corms broke dormancy about the first of January and while growing in nearly total darkness produced roots, stems, leaves and flowers. Dr. John Marr of the Institute of Arctic and Alpine Research at the University of Colorado states that soil temperatures beneath deep snowbanks remain above freezing through the winter. Apparently the laboratory conditions roughly simulated those which the plants encounter in nature.

The snowbank ecology described for *C. lanceolata* is an interesting phenomenon. For example, the stage of development of the plants can be predicted roughly by its distance from the edge of the receeding snowbank. At the margin of the snowbank etiolated but fairly mature plants can be observed. Continuing outward one can find the plants in anthesis, fruits, and moribund at a prescribed distance from the edge of the snowmass. In regions beyond the range of *C. rosea,* however, *C. lanceolata* may also be found associated with other vegetation types. For example, in the Wasatch Mountains of Utah *C. lanceolata* is continuously distributed from the Scrub Oak Community along the lower foothills where it blooms in the early spring, to the Spruce-Fir Community, where it flowers as late as July. However, in these situations it still maintains its association with melting snowbanks or moist areas.

Seasonal—Claytonia rosea usually appears several weeks after the snow cover has melted. The time of emergence naturally varies from year to year; however, at lower elevations along the Colorado Front Range they usually appear between late February and early March. The species flowers into May at the higher elevations where the snow cover remains longer. Populations probably do not remain in flower for more than two or three weeks, and by the end of May it is usually difficult to find individuals of this species blooming at any elevation.

Claytonia lanceolata on the other hand, does not begin to flower until the large snow accumulations begin to melt under the Spruce-Fir Forests, toward the last of May or the first part of June. The species will usually continue to bloom as long as it takes for the snow accumulation areas to melt. This varies with the amount of snow, but is usually complete toward the end of July.

Approximately two to four weeks usually separate the extreme flowering periods for both species. This phenomenon is, of course, a corollary to the fact that the spring melt-out is related to altitude. Seasonal barriers to crossing, therefore, reinforce the effectiveness of ecological isolation between the two species.

Chromosomal—Theoretically, taxa with disparities in chromosome numbers are not expected to produce fully fertile progeny. The individuals of *C. lanceolata* which we have examined cytologically showed that in most cases this species is polyploid where it is sympatric with *C. rosea* (Table 1). These data suggest that barriers to hybridization should characterize these species, but no actual crosses have been made. No evidence suggesting natural hybridization has been encountered.

Summary and Conclusions

Claytonia rosea is distinguished from the related species, *C. lanceolata* with which it has been confused on the basis of the following criteria:

GROSS MORPHOLOGY—*Claytonia* rosea is characterized by possessing basal leaves, whereas *C. lanceolata* has none. The cauline leaves of *C. rosea* are linear to linear-lanceolate. The cauline leaves of *C. lanceolata* are ellipitcal-lanceolate to ovate. The petals apices of *C. rosea* are usally acute, while those of *C. lanceolata* are emarginate. While these characters show a normal range of variation, combinations of these characters will consistently distinguish the two species.

KARYOLOGY—*Claytonia rosea* is a diploid species with a consistent chromosome number of $n=8$. *Claytonia lanceolata*, appears to have variable chromosome numbers, and might possibly have a genetic system similar to the eastern spring beauty, *C. virginica*. In areas where the two species are sympatric *C. lanceolata* is polyploid, but diploid populations of $n=8$ are known in this species beyond the range of *C. rosea*. The species are apparently characterized by distinctive chromosomal systems.

ECOLOGY—*Claytonia rosea* is a species occurring primarily in the Rocky Mountain Montane Forests, in meadows, or beneath stands of Ponderosa Pine, and blooms after the snow has melted. Conversely, *C. lanceolata* generally occurs in the Rocky Mountain Subalpine Forest, at least where it is sympatric with *C. rosea*. However, in areas beyond the range of *C. rosea* it may also occur in other associations. Regardless of the plant community, however, *C. lanceolata* is generally associated with melting snowbanks. Where the species are geographically sympatric, anthesis in the two species generally does not overlap.

If Davis (1966) uses variety in the classical sense, *viz.* for geographically restricted and morphologically definable population systems typically merging with other similar subgroups of the species, then, the available evidence precludes the application of variety to *C. rosea*. The existence of ample, consistent character differences between the two taxa suggest significant evolutionary divergence. Furthermore, they are geographically sympatric, although they are usually not found in close association. When the two taxa do occur near one another, there is absolutely no evidence of hybridization, and the species maintain completely their genetic integrities.

Literature Cited

Abrams, L. 1944. An illustrated flora of the Pacific States, Washington, Oregon, and California. II. Stanford University Press, Stanford.

Cave, M. S., ed. 1964. Index to plant chromosome numbers for 1963. II(8) : 300.

Davis, R. J. 1952. Flora of Idaho. Wm. C. Brown Co., Dubuque.

————. 1966. The North American perennial species of *Claytonia*. Brittonia **18:** (in press).

————. & R. G. Bowmer. 1966. Chromosome numbers in *Claytonia*. Brittonia **18:** 37-38.

Harrington, H. D. 1954. Manual of the plants of Colorado. Sage Books, Denver.

Johnson, A. W. & J. G. Packer. 1963. Cytotaxonomic investigations of the Ogotoruk Creek-Cape Thompson vascular flora. Project Chariot Progress Report, AEC Contract No. AT(04-3)-310. Unpublished Manuscript.

Kearney, T. H. & Peebles, R. H. 1951. Arizona flora. Univ. of Calif. Press, Berkeley and Los Angeles.

Lewis, W. H. 1962. Aneusomaty in aneuploid populations of *Claytonia virginica.* Amer. Jour. Bot. **49:** 918-928.

————. 1966. *In* Chromosome numbers of phanerograms. Ann. Missouri Bot. Gard. **53:** 100.

Munz, P. A. [in collaboration with D. Keck]. 1959. A flora of California. Univ. of Calif. Press, Berkeley and Los Angeles.

Pursh, F. T. 1814. Flora Americae Septentrionalis **1:** 175, London.

Rothwell, N. 1959. Aneuploidy in *Claytonia virginica.* Amer. Jour. Bot. **46:** 353-360.

————. 1965. Chromosome numbers in populations of *Claytonia virginica* from the New York metropolitan area. Amer. Jour. Bot. **52** : 403-407.

———— & C. B. Heiser, Jr. 1951. Chromosome numbers in *Claytonia.* Proc. Indiana Acad. Sci. **60:** 80 (abstract).

Rydberg, P. A. 1904. Studies on the Rocky Mountain flora—XI. Bull. Torrey Bot. Club **31:** 399-410.

Weber, W. A. 1953. Handbook of plants of the Colorado Front Range. Univ. of Colo. Press, Boulder.

Wiens, D. & D. K. Halleck. 1962. Chromosome numbers in Rocky Mountain plants. I. Bot. Not. **115:** 455-464.

POLLEN MORPHOLOGY AND CLASSIFICATION OF THE PYROLACEAE AND MONOTROPACEAE[1]

BY JOAN W. NOWICKE[2]
Department of Botany, Washington University and
Missouri Botanical Garden, St. Louis.

ABSTRACT

Pollen morphology of the *Pyrolaceae* and *Monotropaceae* reinforces the view that the *Pyrolaceae* and *Ericaceae* are closely related and that the *Monotropaceae* should be treated as a distinct family. It further supports the separation of *Moneses uniflora* and *Orthilia secunda* from the genus *Pyrola,* and in the *Monotropaceae* it suggests a realignment of species within the *Hypopitys-Monotropa* complex.

The *Pyrolaceae* as aligned by Schultze-Motel (1964) constitute a diverse group consisting of two subfamilies *Pyroloideae* and *Monotropoideae,* the latter largely saprophytic. Others have reduced one or both taxa to subdivisions of the *Ericaceae,* either as the tribe *Pyroleae* (Bentham & Hooker, 1873), or as the subf. *Monotropoideae* with the *Pyroleae* included in the subf. *Arbutoideae* (Copeland, 1941, 1947). A palynological study was made to determine if pollen morphology, a relatively unused attribute, might better characterize the affinities of the taxa involved.

Erdtman (1952), largely following the systematic treatment of Drude (1889), described the pollen of 15 species representing eight genera. According to him, species of *Pyrola* L. have pollen united in tetrads with individual grains 3-colporate; pollen of *Chimaphila umbellata* Nutt. is in tetrads with apertures not always sharply delimited; pollen of *Moneses uniflora* (L.) Gray also is united in tetrads in which individual grains are 3-colp(oroid)ate; and *Ramischia secunda* (L.) Garcke [=*Orthilia secunda* (L.) House] has single grains which are (2-) 3-colporate. In the *Monotropoideae,* Erdtman described pollen of *Monotropa hypophegea* Wallr. as (2-) 3-colporate, *Pleuricospora fimbriolata* Gray as (3-) 4-colporoidate, *Pterospora andromedea* Nutt. as 4 (-5)-colporoidate, and *Sarcodes sanguinea* Torrey as 4 (-5)-colpate. Erdtman utilized Copeland's (1938) description of *Allotropa virgata* Torrey & Gray which was noted as three-grooved.

Copeland (1934, 1935, 1937, 1938, 1939, 1941, 1947), in an extensive anatomical and systematic study of the tribe *Pyroleae* and subf. *Monotropoideae,* included a brief description of pollen of various genera. In his treatment of the *Pyroleae* (1947), he recognized four genera with the pollen grains of *Ramischia* Opiz (=*Orthilia* Raf.) solitary and tricolpate, those of *Chimaphila* Pursh in easily disrupted tetrads, those of *Pyrola* united in tetrads with the wall of each individual grain "marked by three half-grooves, continued as half grooves on the three as-

---

[1] Supported by Grant No. GB-3825 from the National Science Foundation issued to Dr. Walter H. Lewis.

[2] I wish to thank the curators of the herbaria (MO, F) for the use of herbarium specimens and for the extraction of pollen.

ANN. MISSOURI BOT. GARD. **53**(2): 213-219, 1966.

sociated grains," and grains of *Moneses* Salisb., which Copeland thought tenable as a district genus, also in tetrads.

In his summary article on the *Monotropoideae,* Copeland (1941) divided the group into four, or tentatively five, tribes. The most primitive tribe, *Pterosporeae,* consists of three monotypic genera, viz. *Pterospora* Nutt. with four-grooved pollen (1941), *Sarcodes* Torrey characterized by four-grooved pollen (1941), and *Allotropa* Torrey & Gray with three-grooved pollen (1938). The *Pleuricosporeae,* with only *Pleuricospora* Gray, have four-grooved pollen (1937). The largest tribe, *Monotropeae,* includes: *Monotropsis* Schweinitz in which Copeland (1939) recognized three species having pollen with "a thin exine, smooth except for two grooves lying in the same great circle;" *Hypopitys* Hill which Copeland (1941) believed monotypic [including all five of Small's (1914) species] with two-grooved pollen; *Pityopus* Small described by Copeland (1935) as having solitary grains with smooth walls and germinating through two opposite pores; *Monotropa* L., "apparently monotypic," consisting only of *M. uniflora* L. (Copeland, 1941) and characterized by three-grooved pollen; and two remaining genera, *Monotropastrum* Andres and *Wirtgenia* Andres, were not described. The last tribe, *Hemitomeae,* consists solely of *Hemitomes* Gray, having two-grooved pollen (1941). According to Copeland (1941) possibly a fifth tribe in the subf. *Monotropoideae* should be recognized for the unplaced Oriental genus *Cheilotheca* Hook f.

On a regional basis Erdtman et al. (1961) described the pollen of Scandinavian representatives of the *Ericales,* and Oldfield (1959) characterized the pollen of western European members of this order.

Twelve genera representing 31 species have been examined palynologically. Mature buds, or anthers only, were removed from herbarium specimens and acetolyzed according to the procedure outlined in Erdtman (1952). A complete set of slides is maintained at Missouri Botanical Garden Herbarium with vouchers at either the Missouri Botanical Garden Herbarium (MO) or the Field Museum of Natural History, Chicago (F).

In this survey no attempt is made to revise the species studied, for except as noted the species within each genus are similar palynologically. The specific names used largely follow treatments in the latest floras available.

PYROLACEAE

Pyrola L. (11 species of 40±)

All species examined were essentially similar in pollen morphology. Pollen of *Pyrola secunda* L., treated here as *Orthilia secunda* (L.) House, differs from all species of *Pyrola.*

Grains in tetrads, ca 31μ in diam, individual grains 3-colporate, total adjacent colpi length ca 15.5μ, exine ca 1.7μ in thickness, sexine ± equal to nexine and coarsely reticulated.

Pyrola americana Sweet, *Anderson & Peck s.n.* (MO), Michigan; *P. angustifolia* (Alef.) Hemsl., *Hinton s.n.* (MO), Mexico; *P. aphylla* Smith, *Butler 1575* (MO), California; *P. asarifolia Michx., Heacock 146* (MO), British Columbia;

P. chlorantha Swartz, *Sewell & Weed s.n.* (MO), Labrador; *P. grandiflora* Radius, *Ekblow 591* (MO), Greenland; *P. media* Sw., *Ahlberg s.n.* (MO), "Scandinavia"; *P. minor* L., *Hitchcock & Muhlick 13147* (MO), Montana; *P. rotundiflora* L., *Holm s.n.* (MO), D. C.; *P. sparsifolia Suksdorf, Suksdorf 2695* (MO), Washington; *P. uliginosa* Torrey & Gray, *Cronquist 1744* (MO), Idaho.

Moneses Salisb. (monotypic)

Grains in tetrads, ca 31μ in diam, individual grains 3-colpate, colpi ca 8μ in length, exine ca 2μ in thickness, sexine somewhat thicker than nexine and finely reticulated.

Moneses uniflora (L.) Gray, *Palmer 37563* (MO), S. Dakota.

Orthilia Raf. (monotypic)

Grains single, subprolate, ca 20μ(E) × 15.5μ(P), 3-colporate, colpi ca 13μ in length, ora ca 1.3μ in diam, exine ca 1μ in thickness, sexine ± equal to nexine and finely reticulated.

Orthilia secunda (L.) House, *Thompson & Thompson 601* (F), British Columbia (as *Pyrola secunda* L.)

Chimaphila Pursh (3 species of 4±)

Grains in tetrads (with tetrads tending to clump together after acetolysis), ca 39μ in diam (ca 36μ for *C. umbellata*), individual grains 3-colpate, colpi irregular and vague, exine ca 2μ in thickness (varying from 2.0-2.5μ in *C. occidentalis*), sexine ± equal to nexine and finely reticulated.

Chimaphila maculata (L.) Pursh, *Churchill s.n.* (MO), New Jersey; *C. occidentalis* Rydb., *Mason 7452* (MO), Washington; *C. umbellata* Nutt., *Henderson 5589* (MO), Oregon.

MONOTROPACEAE

Allotropa Torrey & Gray (monotypic)

Grains single, subprolate, ca 23μ × 20μ, 3-colporoidate, colpi ca 13μ in length, ora small, ca 2.5μ in diam, exine ca 1.3μ in thickness, sexine ± equal to nexine and finely reticulated.

Allotropa virgata Torrey & Gray, *Meyer 1120* (MO), Washington.

Pterospora Nutt. (monotypic)

Grains single, prolate spheroidal, ca 22μ × 20μ, 3- to 4-colporoidate, colpi ca 13μ in length, ora narrow and vague (Fig. 1), exine ca 1.8μ in thickness, sexine ± equal to nexine and finely reticulated.

Pterospora andromedea Nutt., *Churchill s.n.* (MO), Michigan.

Sarcodes Torrey (monotypic)

Grains single, ± spheroidal, ca 30μ in diam, 3- to (4-) colp(oroid)ate, colpi ca 11μ in length, ora as one or two weak areas near extremes of colpi (Fig. 2), exine ca 1.8μ in thickness, sexine somewhat thicker than nexine and finely reticulated.

Sarcodes sanguinea Torrey, *Parish 3466* (MO), California.

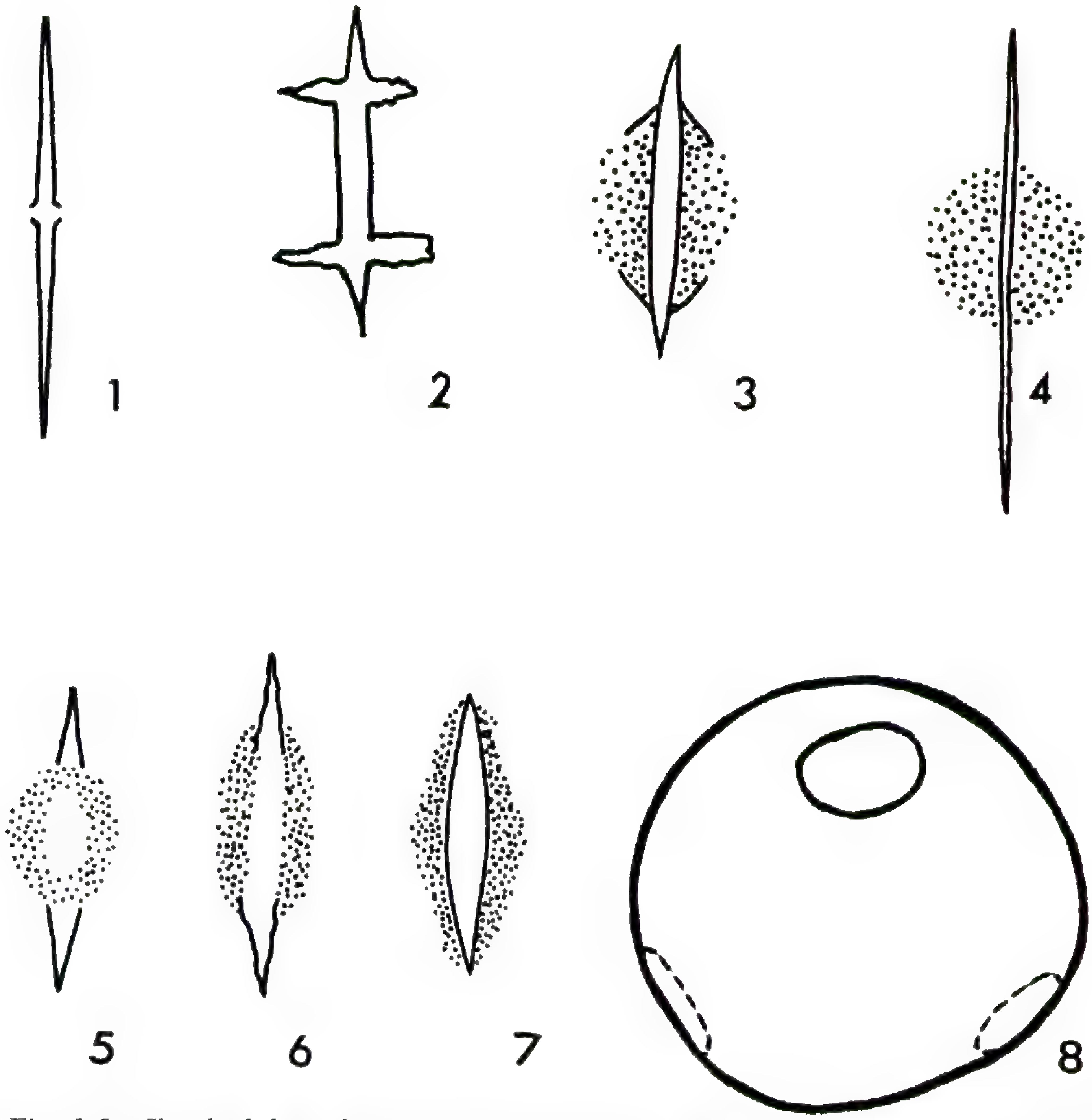


Fig. 1-8. Sketched line drawings of apertures for pollen of *Monotropaceae*. Fig. 1-7, ×3000; Fig. 8, ×1500. Fig. 1. *Pterospora andromedea*. Fig. 2. *Sarcodes sanguinea*. Fig. 3. *Pleuricospora fimbriolata*. Fig. 4. *Monotropsis odorata*. Fig. 5. *Hypopitys monotropa*. Fig. 6. *H. lanuginosa*. Fig. 7. *H. latisquama*. Fig. 8. *Monotropa uniflora* (entire grain).

Pleuricospora Gray (monotypic)

Grains single, ± spheroidal, ca 26μ in diam, (-4) to 5-colporate, colpi ca 10μ in length, ora ca 6μ in length and laterally vague (Fig. 3), exine ca 2μ in thickness, sexine ± equal to nexine and essentially smooth.

Pleuricospora fimbriolata Gray, *Cooke 16129* (MO), California.

Hemitomes Gray (monotypic)

Grains single, prolate spheroidal, ca 28μ × 27μ, (2-) to 3-colporate, colpi ca 14μ in length, ora ca 6.5μ in diam, exine ca 1.5μ in thickness, sexine somewhat thinner than nexine and finely reticulated.

Hemitomes congestum Gray, *Meyer 654* (MO), Washington [as *Newberrya congesta* (Gray) Torrey].

Monotropsis Schweinitz (2 species of 3±)

Grains single, prolate spheroidal, ca 26μ × 24.5μ, 2-colporate, colpi ca 15μ in length, ora ca 5.2μ(length) × 6.5μ(width) as in Fig. 4, exine ca 2μ in thickness, sexine ± equal to nexine and very finely reticulated.

Monotropsis odorata Ell., *Plitt s.n.* (MO), Maryland; *M. reynoldsiae* (Gray) Heller, *Reynolds s.n.* (F), Florida (as *Schweinitzia reynoldsiae* Gray).

Hypopitys Hill (6 species)

H. americana (DC.) Small. Grains single, prolate spheroidal, ca 21μ × 20μ, 2-colporate, colpi ca 12μ in length, ora ca 9μ × 6μ, exine ca 2μ in thickness, sexine ± equal to nexine and finely reticulated.

H. hypophegea (Wallr.) G. Don. Grains single, subprolate, ca 18μ × 21μ, 2- to (3-) colporate, ora irregular in shape but ± equal in length to colpi, exine ca 1.3μ in thickness, sexine almost smooth.

H. lanuginosa (Michx.) Raf. Grains single, ± spheroidal, ca 21μ in diam, 2-colporate, colpi ca 11μ in length, ora ca 6μ × 4μ (Fig. 6), exine ca 1.5μ in thickness, sexine somewhat thicker than nexine and finely reticulated.

H. latisquama Rydb. Grains single, prolate spheroidal, ca 23μ × 22μ, 2- to (3-) colporate, colpi ca 9μ in length, ora ca 8μ × 5μ (Fig. 7), exine ca 1.5μ in thickness, sexine ± equal to nexine and finely reticulated.

H. monotropa Crantz. Grains single, prolate spheroidal, ca 24μ × 22μ, 2- to (3-) colporate, colpi ca 9μ in length, ora ca 4μ in diam (Fig. 5), exine ca 1.3μ in thickness, sexine very finely reticulated.

H. sanguinea Heller. Grains single, flattened on four sides or ± spheroidal, ca 21μ in diam, 2-colporate, colpi ca 11μ in length, ora ca 8μ × 5.5μ, exine variable in thickness from 1.3-2.0μ, sexine ± equal to nexine and finely reticulated.

Hypopitys americana (DC.) Small, *Duncan 9931* (MO), Georgia; *H. hypophegea* (Wallr.) G. Don, *Santesson 14801* (F), Sweden (as *Monotropa hypophegea* Wallr.); *H. lanuginosa* (Michx.) Raf., *Applegate* 3855 (F), California (as *Monotropa lanuginosa* Michx.); *H. latisquama* Rydb., *Meyer 1011* (MO), Washington; *H. monotropa* Crantz, *Holmgrew 1268* (F), Sweden (as *Monotropa hypopitys* L.); *H. sanguinea* Heller, *Blumer s.n.* (MO), Arizona.

Monotropa L. (2 species)

M. coccinea Zucc.. Grains single, oblate spheroidal, ca 27μ × 30μ, 3-porate, ora ca 5.5μ in diam, exine less than 1μ, sexine smooth.

M. uniflora L. Grains single, suboblate, ca 24μ × 28μ, 3-porate, ora ca 6μ × 8μ (Fig. 8), exine less than 1μ, sexine smooth.

The above have been considered as one by several authors (Andres, 1910; Domin, 1915), but minor differences in pollen morphology suggest that they may be distinct.

Monotropa coccinea Zucc., *Johnson* 777 (F), Guatemala; *M. uniflora* L., *Gillett & Findlay* 5469 (MO), Labrador.

Discussion

The status of the *Pyrolaceae* and *Monotropaceae* in relation to the *Ericaceae* and to one another has been a matter of some conjecture. In earlier judgements palynological data have never been fully utilized. The *Pyrolaceae,* with the single exception of *Orthilia secunda,* have grains united in tetrads, mostly 3-colporate with small ora in contrast to the single grains and graded variations of compound and porate apertures observed in the *Monotropaceae.* Such differences reinforce the

treatment in recent floras (Bish, 1952; Bobrov, 1952; Moss, 1959; Clapham et al., 1962) where at least the *Monotropaceae* are considered distinct from the *Pyrolaceae*. For the same reasons the family should also be distinguished from the *Ericaceae*. On the other hand there may be validity in placing the *Pyrolaceae* in the *Ericaceae*, since in an earlier study of more than 250 ericaceous species, I found that the pollen from both taxa were, almost without exception, strikingly similar wih grains united in tetrads and individually 3-colporate. Wodehouse (1932), in examining pollen of a new genus in a related family, the *Clethraceae*, also briefly noted that the *Pyrolaceae* are unquestionably ericaceous. Many authors relegate the taxon to subfamilial or even tribal status under the *Ericaceae* (Bentham & Hooker, 1873; Copeland, 1947; Hitchcock et al., 1959) and my pollen data would support this treatment.

Within the "*Pyrolaceae*" most of the species in each genus are almost identical in pollen morphology. Two exceptions occur in species formerly placed with *Pyrola*. *Moneses uniflora*, thought by Copeland (1947) to be tenable as a distinct genus, has pollen united in tetrads like most members of the "family", but is atypical in *Pyrola* for the grains lack an os and are only 3-colpate. Considering the conservative pollen morphology of most species of *Pyrola*, this divergence could well represent a character significant at the level of genus. *Orthilia secunda* is the only species to have single grains; it should also be set apart from *Pyrola* in agreement with House (1921).

In the *Monotropaceae*, although a wide range of aperture types is represented, there exists a graded sequence in the variation present. The *Pterosporeae* were considered by Copeland (1941) as the most primitive tribe, and their pollen morphology, mostly 3-colporoidate, reinforces this view. *Sarcodes*, with its ora usually represented by two weak areas near the extremes of the colpus, a condition accentuated by acetolysis also present to a lesser degree in grains treated only with 2% acetic-orcein, may represent an evolved palynological condition though otherwise resembling *Allotropa* and *Pterospora*.

With the exception of *Monotropa*, the remaining genera studied, *Pleuricospora*, *Hemitomes*, *Monotropsis*, and *Hypopitys*, possess pollen with a second type of aperture. This is colporate in which the extent of the os and the sharpness of its delimitation, as well as aperture number, parallel somewhat the established generic alignments. *Pleuricospora*, although considered advanced in the number of apertures, has nevertheless, an os which because of its lateral vagueness, may mark the most primitive genus in respect to pollen morphology. *Hemitomes* and *Monotropsis*, while differing somewhat in their colpus length, have a more or less circular os which is well delimited.

Within those species grouped in *Monotropa* (Moss, 1959; Clapham et al., 1962; Schultze-Motel, 1964) the morphology of the pollen represents two highly divergent forms. The pollen of the one group, including the type of *Hypopitys*, *H. monotropa* Crantz, is 3-colporate and mostly prolate spheroidal, whereas the pollen of the second group, including the type of *Monotropa*, *M. uniflora* L., is 3-porate and oblate spheroidal or suboblate. This agrees with Copeland's (1941) separation of

the genera. However, he concluded that both were monotypic but, even from the examination of pollen alone, differences between species of *Hypopitys* (Fig. 5, 6, 7) and between *M. uniflora* and *M. coccinea* are noteworthy, and for the present are considered as separate species.

Palynologically *Monotropa* is the most distinct member of the *Monotropaceae* (Fig. 8) and probably the most highly evolved. It is the only representative of the third pollen type, 3-porate, otherwise rare in the *Ericales*.

Literature Cited

ANDRES H. 1910. Die *Pirolaceae* des Aschersonschen Herbariums. Bot. Verein Prov. Brandenberg **52**: 90-95.

BENTHAM, G. and J. D. HOOKER. 1873. *Ericaceae* & *Monotropeae*, p. 577-608, Genera Plantarum **2**.

BISH, N. A. 1952. *Pyrolaceae*, p. 7-19, *In* Flora of U.S.S.R. Vol. **18.**

BOBROV, E. G. 1952. *Monotropaceae*, p. 19-22, *In* Flora of U.S.S.R. Vol. **18.**

CLAPHAM, A. R., T. G. TUTIN & E. F. WARBURG. 1962. Flora of the British Isles. Cambridge University Press.

COPELAND, H. F. 1934. The structure of the flower of *Newberrya*. Madroño **2**: 137-142.

————. 1935. On the genus *Pityopus*. loc. cit. **3**: 154-168.

————. 1937. The reproductive structures of *Pleuricospora* loc. cit. **4**: 1-16.

————. 1938. The structure of *Allotropa*. loc. cit. 137-153.

————. 1939. The structure of *Monotropsis* and the classification of the *Monotropoideae*. loc. cit. **5**: 105-118.

————. 1941. Further studies on *Monotropoideae*. loc. cit. **6**: 97-119.

————. 1947. Observations on the structure and classification of the *Pyroleae*. loc. cit. **9**: 65-102.

DOMIN, K. 1915. Vergleichende Studien uber den Fichtenspargel. Sitzungsb. kgl. bohm. Ges. Wiss. Prag., II Kl., I Stück: 1-111.

DRUDE, O. 1889. *Pirolaceae*, *In* ENGLER & PRANTL, Nat. Pflanzenf. IV. **1**: 3-11.

ERDTMAN, G. 1952. Pollen morphology and plant taxonomy. Angiosperms. Almqvist & Wiksell, Stockholm.

————, B. BERGLUND & J. PRAGLOWSKI. 1961. An introduction to a Scandinavian pollen flora. Almqvist & Wiksell, Stockholm.

HITCHCOCK, C. L., A. CRONQUIST, M. OWNBEY, & J. W. THOMPSON. 1959. Vascular plants of the Pacific Northwest. Part 4. Univ. of Washington Press, Seattle.

HOUSE, H. D. 1921. Nomenclatorial notes on certain American plants. I. Amer. Midl. Nat. **7**: 126-135.

MOSS, E. H. 1959. Flora of Alberta. Univ. of Toronto Press, Toronto.

OLDFIELD, F. 1959. The pollen morphology of some of the West European *Ericales*. Pollen et Spores **1**: 19-48.

SCHULTZE-MOTEL, W. 1964. *Pyrolaceae*, p. 381-383, *In* ENGLER, Syllabus der Pflanzenf. **2.** Gebrüder Borntraeger, Berlin.

SMALL, J. K. 1914. *Monotropaceae*, p. 11-18, *In* North American Flora. Vol. **29**.

WODEHOUSE, P. G. 1932. *In* SMITH & STANDLEY, *Schizocardia*, a new genus of trees of the family *Clethraceae*. Trop. Woods **32**: 8-11.

SYSTEMATIC IMPLICATIONS FROM ELECTRON MICROSCOPIC STUDIES OF COMPOSITAE POLLEN—A REVIEW[1]

BY JOHN J. SKVARLA[2] AND B. L. TURNER[3]
Department of Botany & Microbiology, University of Oklahoma, Norman and
Department of Botany, University of Texas, Austin

ABSTRACT

A discussion is presented of the pollen ultrastructure of 184 species from 11 *Compositae* tribes. For the *Vernonieae, Astereae, Inuleae, Arctotideae, Mutisieae* and *Cichorieae* the data represent an initial effort at defining the morphological parameters of these tribes. For the *Heliantheae, Ambrosieae, Helenieae, Anthemideae* and *Senecioneae* supplemental data obtained from current studies augment previous observations made for these tribes. Although ultrastructural characters are given primary emphasis, light microscope observations, particularly the analyses of sectioned pollen walls, are also included. The results of our work are discussed in relation to taxonomy and phylogeny within the *Compositae*.

INTRODUCTION

The recognition of the electron microscope as an indispensable adjunct to light microscopic interpretations of pollen grain walls (exines) became obvious through the work of several investigators (Fernández-Morán & Dahl, 1952; Mühlethaler, 1953; Afzelius, Erdtman & Sjöstrand, 1954). The most significant finding of these pioneering studies was that ultra-thin sectioned exines revealed internal structures which were defined poorly or not at all by light microscopy. Recognizing the potential that the electron microscope held for the areas of pollen development, morphology and possibly taxonomy, Rowley (1959), using a background of light microscopic knowledge, applied electron microscopy to the *Commelinaceae*. Although a major part of his study was developmental in nature, it was nevertheless one of the first studies to make detailed comparisons among closely related genera and species. While Rowley did not find as much variation in the *Commelinaceae* as we have noted in the *Compositae*, he was able to detect some differences not previously recorded through the use of light microscopy.

The external morphology of pollen walls in the *Compositae* has been scrutinized by Wodehouse in a series of light microscopic investigations beginning in

---

[1]Presented as part of a symposium on Pollen Morphology and Plant Taxonomy before the joint meeting of the American Society of Plant Taxonomists and the Systematic Section of the Botanical Society of America, at the 16th annual meeting of the American Institute of Biological Sciences, held at the University of Illinois, Urbana, August 18, 1965.

[2]This investigation constitutes a portion of a Ph.D. study completed at The University of Texas as well as continued research in The Department of Botany and Microbiology, The University of Oklahoma. The authors express their appreciation to the Central Stenographic Service, University of Oklahoma, for typing of the manuscript, and to Dr. R. W. Lent, University of Oklahoma, for assistance with sketches 1-9.

[3]Supported in part by grant funds from NSF GB-1216.

Publication aided by funds from the authors.

ANN. MISSOURI BOT. GARD. **53**(2): 220-256, 1966.

1926 and extending through 1945. These investigations did little to elucidate the internal features of the pollen wall, and it remained for Stix (1960), employing ultraviolet microscopy on sectioned pollen, to describe for the first time the internal morphology. Her descriptions, made from species representing all 13 tribes in the *Compositae,* showed a complexity of internal patterns which, in some instances, could be correlated with the external patterns shown by Wodehouse. She also showed that many of the pollen grains with superficially similar external surfaces were different internally. Stix recognized 42 "pollen types" in the *Compositae,* but no attempt was made to relate these types to specific tribal or phyletic lines.

With the above studies as a base, we have undertaken electron microscopic investigations in the *Compositae.* We should emphasize at the outset that our work is done in concert with light microscopic observations on whole pollen mounts and on 1μ-sectioned pollen grains. In addition to obtaining higher resolution with the electron microscope, our approach contrasts with the ultraviolet work in that we have attempted to examine systematically a larger number of taxa before assigning pollen types. Below are listed the species of *Compositae* we have examined with the electron microscope arranged by tribes following Hoffman (1897).

1. Vernonieae: *Vernonia pacchensis* Benth.

2. Astereae: *Aphanostephus kidderi* Blake, *A. ramosissimus* DC., *A. riddellii* T. & G., *A. skirrhobasis* (DC.) Tuel., *Astranthium* sp., *Baccharis decussata* (Klatt) Hieron., *Bellis* hybrids, *Erigeron* sp., *Solidago speciosa* Nutt.

3. Inuleae: *Anaphalis margaritacea* var. *occidentalis* Greene, *Craspedia richea* Cass., *Dimeresia howellii* Gray, *Inula britannica* L.

4. Heliantheae: *Argyroxiphium virescens* H.B.K., *Aspilia* sp., *Baldwinia uniflora* Nutt., *Balsamorhiza hookeri* Nutt. var. *neglecta* (Sharp) Cronq., *Baltimora recta* L., *Bebbia juncea* (Benth.) Greene, *Bidens laevis* (L.) B.S.P., *Calea urticifolia* (Mill.) DC., *Calycadenia multiglandulosa* DC. subsp. *cephalotes* Keck, *Clibadium arboreum* J. D. Smith, *Coreopsis cardaminaefolia* (DC.) T. & G., *Cosmos bipinnatus* Cav., *Dahlia coccinea* Cav., *Echinacea pallida* Nutt., *Eclipta alba* (L.) Hassk., *Engelmannia pinnatifida* Gray, *Galinsoga ciliata* (Raf.) Blake, *Geraea canescens* T. & G., *Guardiola mexicana* H. & B., *Helianthus annuus* L., *Heliopsis annua* Hemsl., *Hemizonia corymbosa* (DC.) T. & G., *Hidalgoa ternata* Llave, *Jaegeria hirta* (Lag.) Less., *Lagascea decipiens* Hemsl., *Layia glandulosa* (Hook.) H. & G., *Marshallia caespitosa* Nutt., *Melampodium cinereum* DC., *M. leucanthum* T. & G., *Milleria quinqueflora* L., *Notoptera epalacea* (Hemsl.) Blake, *Parthenice mollis* Gray, *Parthenium hysterophorus* L., *P. incanum* H. B. K., *Polymnia maculata* Cav., *Rudbeckia laciniata* L., *Salmea scandens* (L.) DC., *Silphium astericus* L., *Spilanthes americana* L. var. *parvula* (Rob.) A. H. Moore, *S. americana* Hieron, *Thelesperma megapotamicum* (Spreng.) Kuntze, *Tridax balbisioides* (H.B.K.) Gray, *Varilla mexicana* Gray, *Verbesina persicifolia* DC., *Viguiera dentata* (Cav.) Spreng., *Wedelia biflora* (L.) DC., *Wyethia arizonica* Gray, *Ximenesia encelioides* Cav., *Zinnia angustifolia* H.B.K.

5. Ambrosieae: *Ambrosia artemisiifolia* L., *A. confertiflora* DC., *A. cumanensis* H.B.K., *A. grayi* (A. Nebr.) Shinners, *A. psilostachys* DC., *A. trifida* L., *Dicoria*

brandegei Gray, *D. canescens* T. & G., *Euphrosyne parthenifolia* DC., *Franseria acanthicarpa* (Hook.) Cav., *F. bryantii* Curran, *F. confertiflora* (DC.) Rydb., *F. tenuifolia* Harv. & Gray, *F. tomentosa* Gray, *Hymenoclea fasciculata* Nels., *H. monogyra* T. & G., *H. salsola* T. & G., *Iva acerosa* Nutt., *I. ambrosiaefolia* Gray, *I. ambrosiaefolia* Gray subsp. *ambrosiaefolia, I. ambrosiaefolia* subsp. *lobata* (Rydb.) Jackson, *I. angustifolia* Nutt., *I. annua* L., *I. annua* L. var. *annua, I. annua* var. *caudata* (Small) Jackson, *I. asperifolia* L., *I. axillaris* Pursh, *I. cheiranthifolia* H.B.K., *I. dealbata* Gray, *I. fructescens* L., *I. fructescens* L. subsp. *fructescens, I. fructescens* subsp. *oraria* (Bartl.) Jackson, *I. hayesiana* Gray, *I. imbricata* Walt., *I. nevadensis* Jones, *I. texensis* Jackson, *I. xanthifolia* Nutt., *Oxytenia acerosa* Nutt., *Xanthium canadense* Mill., X. *chinense* Mill., X. *commune* Britton, X. *italicum* Moretti, X. *pennsylvanicum* Wallr., X. *speciosum* L., X. *spinosum* L., X. strumarium L.

6. HELENIEAE: *Amblyopappus pusillus* H. & A., *Baeria maritima* Gray, *Bahia nudicaulis* Gray, *Cacosmia rugosa* H.B.K. var. *arachnoides* Hier., *Espejoa mexicana* DC., *Gaillardia pulchella* Foug., *Hulsea carnosa* Rydb., *Hymenopappus newberryi* (Gray) Johnston, *Jaumea peduncularis* (H. & A.) Oliv. & Hieron., *Lasthenia chrysostoma* (F. & M.) Greene, *L. coronaria* (Nutt.) Ornduff, *L. glabrata* Lindl. subsp. *glabrata, Monolopia lanceolata* Nutt., *Palafoxia hookeriana* T. & G., *Pericome caudata* Gray, *Pseudoclappia arenaria* Rydb., *Philostrophe villosa* Rydb., *Sartwellia mexicana* Gray, *Venegasia carpesioides* DC.

7. ANTHEMIDEAE: *Aaronsohnia factorovky* Warb. & Eig., *Achillea lanulosa* Nutt., *Anthemis arvenis* L., *A. cotula* L., *A. micheliana* Guss., *A. paranassica* Boiss., *A. ruthenica* M. & B., *A. tinctoria* L., *Artemisia absinthium* L., *A. annua* L., *A. arbuscula* Nutt., *A. cana* Pursh subsp. *viscidula* (Osterhout) Beetle, *Chrysanthemum leucanthemum* L. var. *pinnatifidum* Lecog. & Fam., *C. maximum* Ramond, *C. parthemium* (L.) Bernh., *Crossostephium turkestanicum* A. & S., *Leucanthemum gussonii* Nym., *Matricaria chamomilla* L., *Tanacetum camphoratum* L.

8. SENECIONEAE: *Bartlettia scaposa* Gray, *Blennosperma bakeri* Roderick, *B. californica* T. & G., *B. chilense* Less., *B. chilense* Less. × *bakeri* Heiser, *B. nanum* (Hook.) Blake, *Crocidium multicaule* Hook., *Emilia coccinea* (Sims) Sweet, *Euryops tenuissimus* Less., *Gynoxys parvifolia* Cautr., *Gynura pseudochina* (L.) DC., *Haploesthes greggii* Gray, *Liabum caducifolium* Rob. & Bartl., *L. kluttii* Rob. & Greenm., *Petasites hyperboreus* Rydb., *Peucephyllum schottii* Gray, *Psathyrotes annua* (Nutt.) Gray, *Schistocarpha bicolor* Less., *S. platyphylla* Greenm., *S. sinforosii* Cuatr., *Senecio ampullaceus* Hook., *S. coymolachensis* Cabrera, *S. glabellus* Poir., *S. loeseneri* Hieron., *S. riddellii* T. & G., *S. verticellatus* Klatt., *Sinclairia hypoleuca* (Greenm.) Rydb., *Tetradymia canescens* DC., *Werneria stuebellii* Hieron.

9. ARCTOTIDEAE: *Arctotis stoechdifolia* Berk., *Berkheopsis diffusa* (Oliv.) Hoffm., *Didelta* sp.

10. MUTISIEAE: *Moquinia volutina* Bong., *Mutisia campanulata* Less.

11. CICHORIEAE: *Andryala* sp., *Pyrrhopappus carolinianus* (Walt.) DC., *Sonchus* sp.

Preparation of Pollen Walls

All pollen samples were removed from herbarium sheets and processed for electron microscopy according to previously described methods (Skvarla, 1966). In brief, these methods consist of (1) acetolysis, (2) staining with buffered OsO_4, (3) post-staining with aqueous uranyl acetate, (4) embedding in Araldite-Epon resins, (5) sectioning with diamond knives, and (6) section staining with lead citrate. For light microscopy the acetolyzed exines were prepared according to techniques of Wilson & Goodman (1963, 1964).

Morphology of Compositae Pollen Wall

Acetolyzed pollen walls (i.e. pollen walls chemically treated to remove protoplasm as well as tapetal debris, etc.) sectioned at approximately $1/40\mu$ are differentiated with the electron microscope into two major layers, a unipartite layer and a tripartite layer, as sketched in Fig. 1.

The unipartite layer is located on the interior surface of the pollen wall (i.e. the surface nearest the protoplasmic region) and is termed the endexine. The tripartite layer is known as the ektexine and is depicted above as consisting of (1) foot layer, (2) columellae and (3) tectum with associated spinules.

The terminology employed to describe these pollen wall layers is adopted from the light microscopic work of Faegri (1956); we feel that it serves to bridge the gap in expressing concepts developed in both light and electron microscopy. By using light microscopic staining (basic fuchsin), Faegri observed the ektexine to stain darkly while the endexine showed little staining; our methods employing electron stains (OsO_4) also showed identical stain differentiation. It is apparent from this that the pollen wall is structured into at least two layers which become

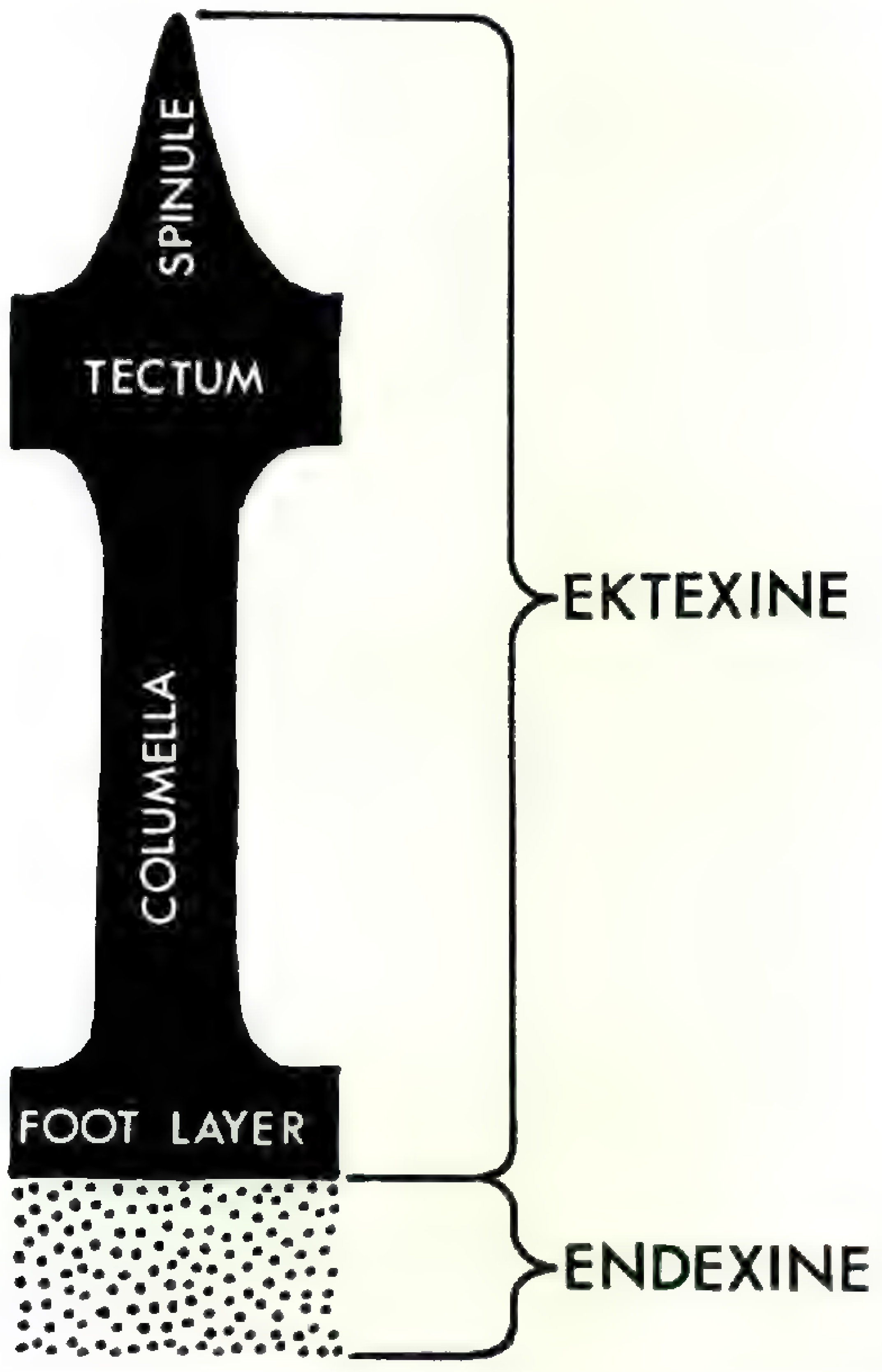


Fig. 1. Basic stratification layers in *Compositae* pollen walls.

accentuated by staining. A similar image can be obtained when acetolyzed exines are left unstained: the electron microscopic image shows the same two layers, although with loss of contrast.

The foregoing description serves as an introduction to the morphology of the *Compositae* by defining the layers common to all taxa. Figure 1 schematically depicts the general features of *Compositae* pollen; however, as will be shown subsequently, different and complex configurations are widespread in the family. Due to the intricacy of morphological organization, these layers will be discussed initially on an individual basis, and only when clarity demands it will reference be made to specific taxa. Following this discussion we shall summarize the ultrastructural morphology at the tribal level (p. 000), emphasizing the significance of these layers as they relate to taxonomic and phylogenetic problems.

Endexine. To date primary attention to endexine has been focused on the great variability in its thickness. This variability is analyzed from two aspects: (1) the thickness in comparison with that of the overlying foot layer, and (2) inherent thickness differences exclusive of foot layer considerations (i.e. endexine thickness of one taxon vs. that of another taxon). Of the two aspects, the former is by far the more significant as closely related taxa can be differentiated by estimating comparative endexine-foot layer thicknesses and establishing approximate ratios (given in tribal discussions).

We have not attempted to quantify these measurements beyond visual estimations because of the difficulty in obtaining properly oriented sections. As valid measurements would require that the same site be measured in all taxa, the obvious solution would be to use median sections. This approach is presently unfeasible, however, owing to the difficulties in obtaining such sections. In addition, the endexine is not always represented as a "complete" morphological entity. It had been determined previously (Skvarla & Larson, 1965a) that the lower surface of the endexine in some *Heliantheae* may appear to be incomplete or disrupted. More recent studies have shown that in the *Helenieae* and *Senecioneae* the common occurrence of disrupted lower endexine surfaces makes it necessary to reconstruct the endexine from various sectional views before ratios can be estimated (Skvarla & Turner, 1966). Still another factor complicating ratio estimation, and as yet not completely investigated, is that of the endexine serving as a host for foot layer lamellae in some taxa (Skvarla & Larson, 1965b). The problem is in the uncertainty as to the dividing line between the endexine and the foot layer. While this observation might hearten those groups favoring endexine-foot layer as the same morphological unit, we believe that previously discussed stain and ultrastructural observations obviate such a distinction, and tend more to stress the need for developmental studies before morphological terminology can be unequivocally applied. It is our feeling, however, that the concept of neat divisions between pollen wall layers, at least in some taxa, can no longer stand unchallenged.

Concerning inherent endexine thicknesses it is only necessary to comment that while the endexine is variable in thickness from one tribe to the next, it is generally of uniform dimensions for taxa of a tribe.

In addition to the above discussed foot layer lamellations, the endexine has been observed to contain indigenous lamellae. These lamellae are present in all areas of the endexine: in intercolpial areas they serve the purpose of harmomegathic mechanisms (i.e. expansion-contraction in response to temperature and moisture fluctuations), while in the regions of the germinal apertures the lamellae are more densely concentrated and serve as an aid to pollen tube exitus. Caution has been used in attempting to correlate lamellar patterns with specific taxa, as it is becoming evident that lamellae are obscured by acetolysis (Skvarla, in preparation). Figure 2 summarizes some of the above discussed characteristics of the endexine.

Before leaving the discussion of the endexine a few supplementary comments seem necessary in the light of investigations now in progress. First, the endexine may not be as uniform on its exterior surface (i.e. the area in contact with the foot layer) as has so far been thought. In the tribe *Vernonieae* (discussed in more detail below) the endexine is seen to bulge directly under the columellar-foot layer regions of the ektexine. It is tempting to compare this endexine bulging with a similar effect on foot layers of the *Heliantheae;* however, the respective exines are grossly different in other morphological characters.

A second observation is that the endexine may be composed of two layers. The concept of more than one endexine layer has been sharply debated and, unfortunately, at times, inconclusively supported. We are not interested in extending this controversy; it is already overworked. Our original skepticism concerning the existence of more than one endexine layer resulted from observations employing potassium permanganate as an electron stain (Larson & Skvarla, 1961). With this stain the endexine occasionally showed a narrow opaque band on the lower surface, and because little comparative information was available at that time, the layer was suggested as being equivalent to the endonexine described by Erdtman (1960). (In our terminology this would simply mean a second endexine layer.) However, the possibility of artifact also was taken into consideration.

The situation appears to be different with the species examined in the *Mutisieae,* since various stains, uniformly delineated a second endexine layer. A new name is not given to it, as nothing is known about its formation and very little about its distribution in the *Compositae;* therefore, we simply refer to the endexine in such cases as being bi-layered.

Ektexine: *Foot Layer.* The complexities of morphological organization and variation of the endexine are rivaled by that of the ektexine. The basal unit of the ektexine, the foot layer, has been discussed already in terms of its most important character, that of thickness ratio with reference to the endexine. Like the endexine, intrinsic foot layer thicknesses vary among taxa, but unlike it, always in a more pronounced manner. In addition to the previously mentioned basal lamellae of some species, two other distinguishing features have been noted in the foot layer. The first is a doming or bulging along irregular intervals at the upper surface (Skvarla & Larson, 1965a). The doming is usually observed beneath a spine region and is restricted to taxa in which a separation (i.e. a cavus, to be discussed below)

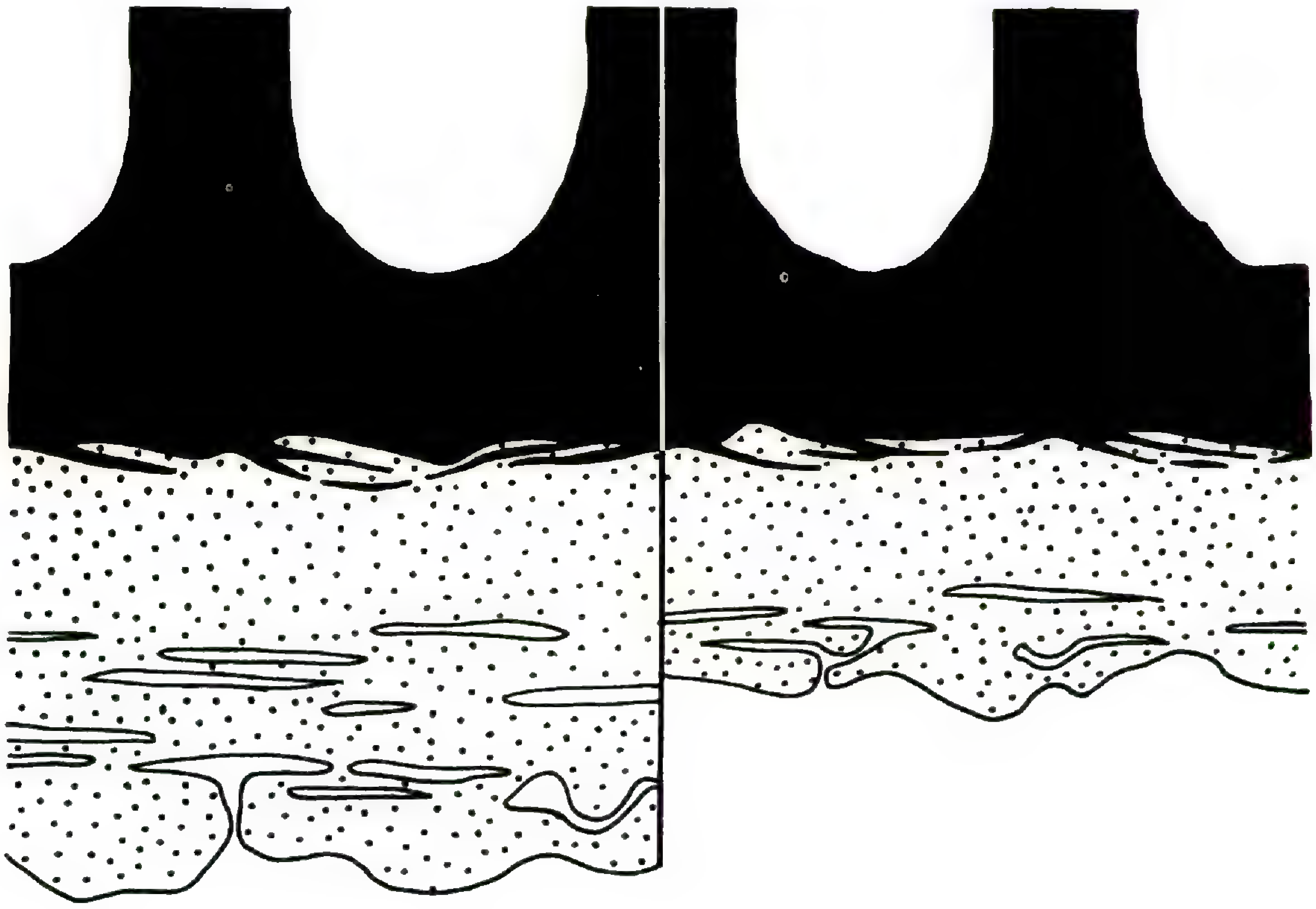


Fig. 2. Morphological characteristics of the endexine. The variability of endexine thickness is contrasted by adjacent sketches. The lower endexine surface is often highly irregular and disrupted. Intergrading foot layer lamellae are present in the upper portion of the endexine. Indigenous lamellae are dispersed throughout the endexine.

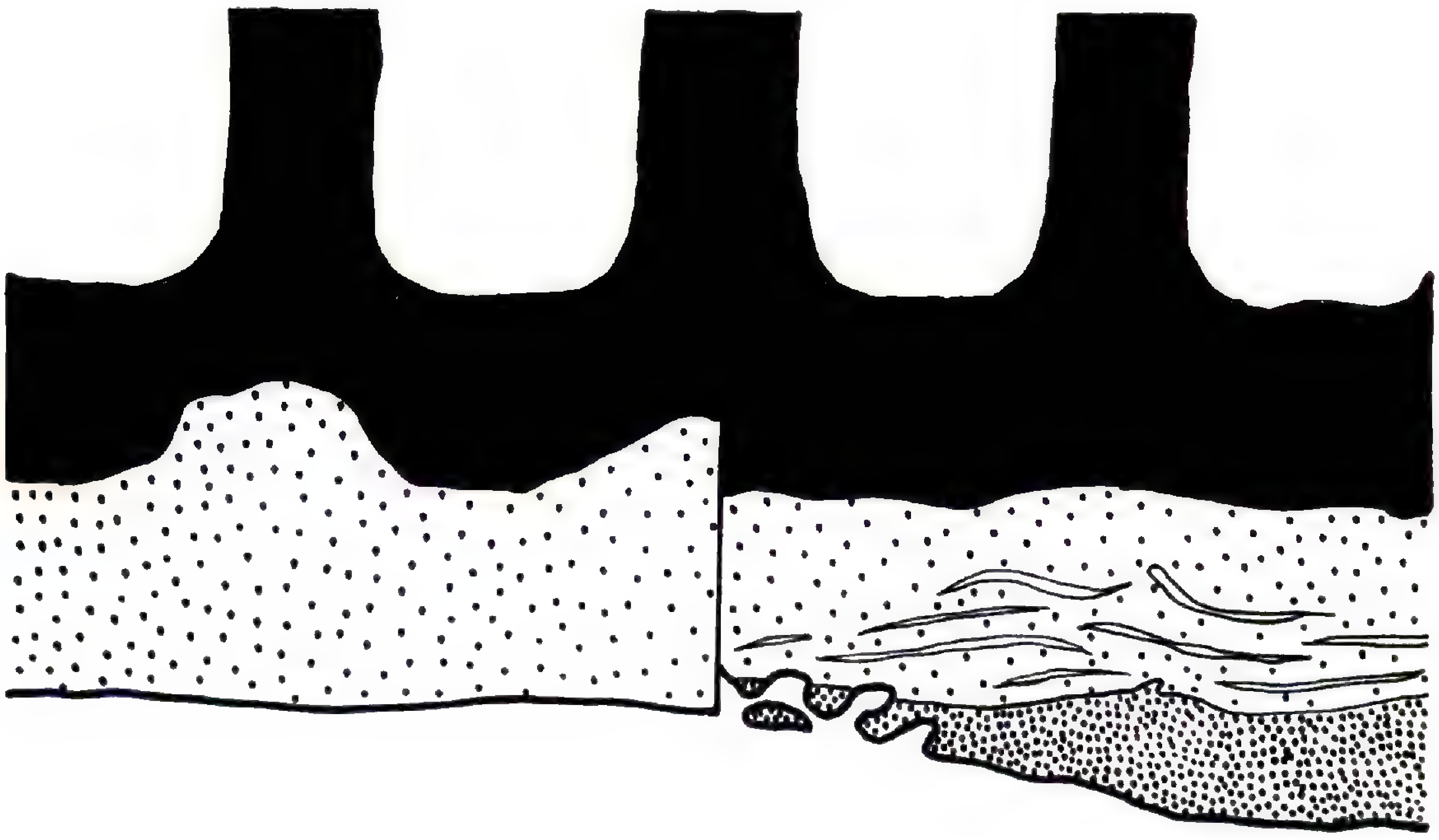


Fig. 3. Endexine peculiarities. Endexine at left shows a doming beneath columellar areas; at the right the endexine is bi-layered.

between the columellae and foot layer can be distinguished. Owing to its common occurrence in many taxa, it does not appear that foot layer doming will have taxonomic application.

A second and presently less well understood feature is that the foot layer in certain species contains areas of microfibrils concentrated into lamellar zones. These zones are located near the basal portions of the foot layer and can be traced with considerable regularity. Although the foot layer has been found to possess lamellar organization (Skvarla & Larson, 1965a, 1965b), such lamellae have been attributed to a splitting of the lower surface of the foot layer and subsequent interdigitation with the endexine. In our present work, the microfibrils are positioned within the foot layer and cannot be interpreted as originating from a splitting of the lower surface. It is noteworthy that of the two species in which it has been observed so far (*Cacosmia* and *Liabum*, to be described below), a close taxonomic relationship has been postulated by the junior author on other than pollen morphology, in spite of the fact that the species are currently assigned to different tribes.

Cavus. The separation between the columellae and foot layer is a major characteristic of several taxa (including tribes). This separation has been termed a cavus (Skvarla & Larson, 1966a), and is another example of attempting to integrate electron and light microscopic observations. The term was adopted from Iversen & Troels-Smith (1950), but is slightly modified since we interpret the cavus to separate ektexine units; the above named investigators consider the cavus as being interposed between the ektexine and endexine. Because the cavus has been used to delineate numerous taxa, we will present here a brief summary of previous work with this character. Although Wodehouse was principally concerned with describing the external features of the *Compositae* pollen wall, he did illustrate a few species in the *Heliantheae-Ambrosiinae* as bladdered or winged in optical views (1928a, 1935). In Stix's thin section work many species were clearly diagrammed in this bladdered condition, showing a distinct separation in the pollen wall. This separation and the pollen layers associated with it were interpreted as the "hohlraum" (hole) surrounded on one side by the nexine 1 (the upper layer of a two-layered endexine according to terminology of Erdtman, 1960) and on the other side by the columellae: in other words, the hohlraum divided the endexine from the ektexine. Additionally the basal extremities of the columellae were always shown to be connected laterally by a uniform layer termed the "stutzmembran" (supporting membrane), presumably the lower-most member of the ektexine.

Initial electron microscopic observations made in the *Heliantheae* (Skvarla & Larson, 1965a) also disclosed that in intercolpial areas the columellae were free from union with the main body of the pollen grain. The layer immediately below the separation (hohlraum) has already been discussed as the foot layer (not a second endexine layer) and need not be considered further. The area in question concerns the columellae, particularly the columellar-stutzmembran association. With the electron microscope it has been possible to distinguish (1) columellae with continuously connected basal regions (i.e. with a stutzmembran), (2) colu-

mellae with intermittently connected basal regions, and (3) columellae completely lacking in basal connections (i.e. without stutzmembran). In the latter case the columellae may have club-shaped or distended basal ends. The disposition of the columellar connections serves to illustrate what has been stressed at several junctures in this symposium, that of the need for developmental studies. This can be illustrated by the following interpretations: the stutzmembran "layer" can be considered (1) part of the original foot layer which became detached during the ontogeny of the cavus, (2) a second stratum of the foot layer, or (3) an inherent part of the columellae. Figure 4 depicts these various relationships.

Columellae. The columellae, which display considerable morphological diversity, constitute a significant criterion for separating many taxa. For example, Stix (1960) has emphasized this character in her recognition of pollen types in the *Compositae.* Although the light microscope is inferior to the electron microscope in resolving columellar structure, by using 1μ sections, we were able to distinguish some columellar variations. In our electron microscopic work several types of patterns emerged which confirmed and further refined our 1μ sectioned observations. These patterns are as follows:

(1) *Solid, single level columellae.* Columellae in this category are essentially straight solid rods, which in caveate exines may assume basally any or all three of the above described forms (i.e. connected, intermittently connected, disconnected, and distally may form either a completely connected tectum or a partially connected tectum. When the columellae branch or fork basally, they are described as conjunct; when they fork distally they are digitate.

(2) *Foraminate, single level columellae.* Distinguished from the first category in that holes characterize columellae and columellar basal connections. These holes, called "internal foramina" (Skvarla & Larson, 1965a) have proven to be of systematic importance, as they are often restricted to specific taxa (including tribes). The term was introduced to distinguish these structures from a system of plasmodesmata through the pollen wall which has been recognized by several investigators (Afzelius, in Erdtman, 1952; Rowley et al., 1959; Chambers & Godwin, 1961; etc.).

Although the internal foramina are generally empty, sometimes they are seen to be filled. The filling is usually precipitated by OsO_4 when this stain is employed; without staining, the filling is an ill-defined black, amorphous mass. We do not believe the fillings are of a cytoplasmic nature, as acetolysis removes such materials. At present it appears that it is extraneous tapetal debris, or possibly oil droplets not completely destroyed during chemical treatment. To date, internal foramina have been found only in caveate exines having a single level of columellae.

(3) *Solid, double level columellae.* Columellae in this group are typified by a digitation and subsequent horizontal branching. Although the digitating branches can be initiated at any position on the columella, usually they are found no lower than at the approximate mid-length. From positions at which the branches originate they can be traced laterally to where various degrees of fusion occur with

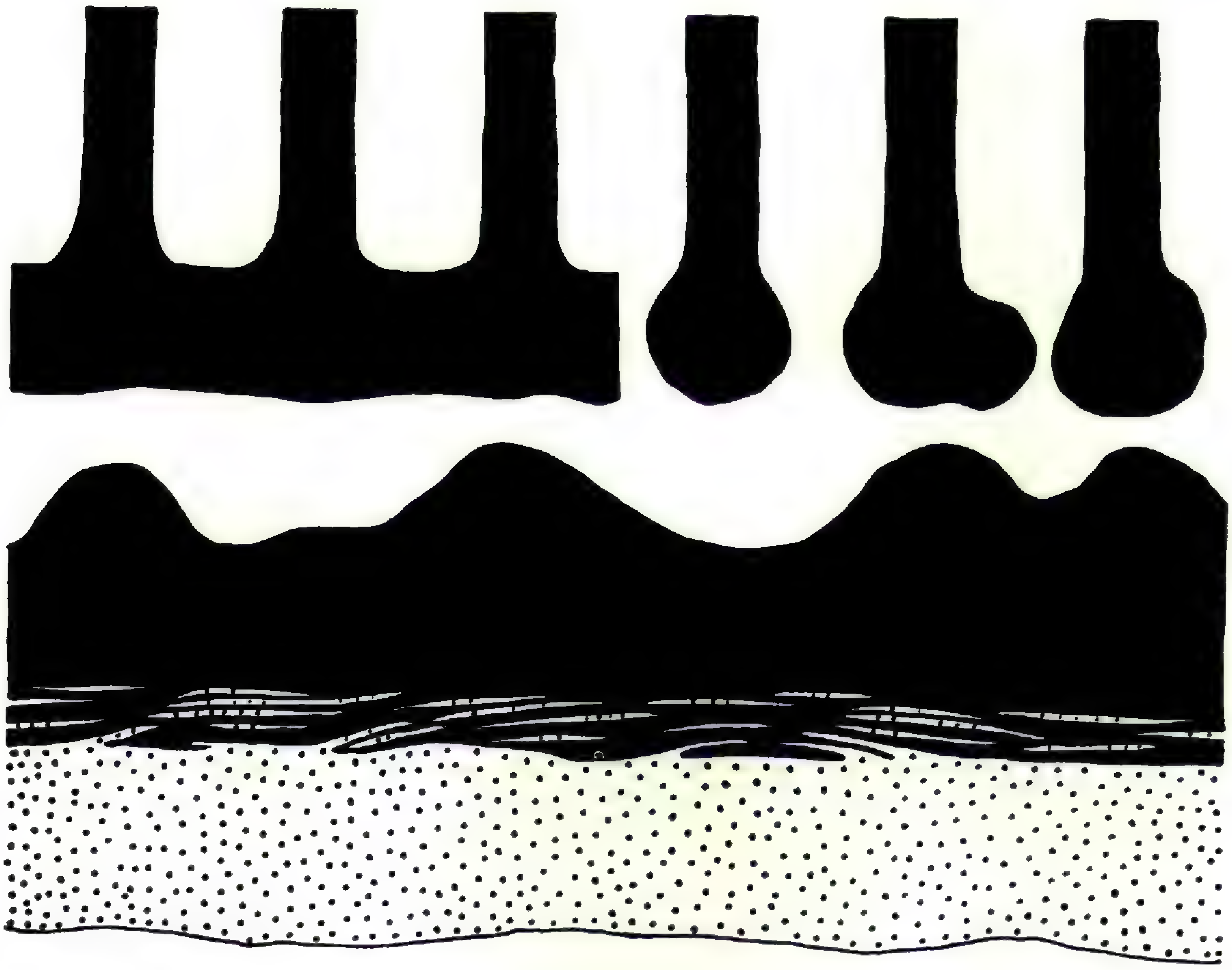


Fig. 4. Morphological characteristics of the foot layer and columellar bases. At left the columellae are connected basally; at right columellar bases are disconnected. A cavus separates columellae from domed foot layer.

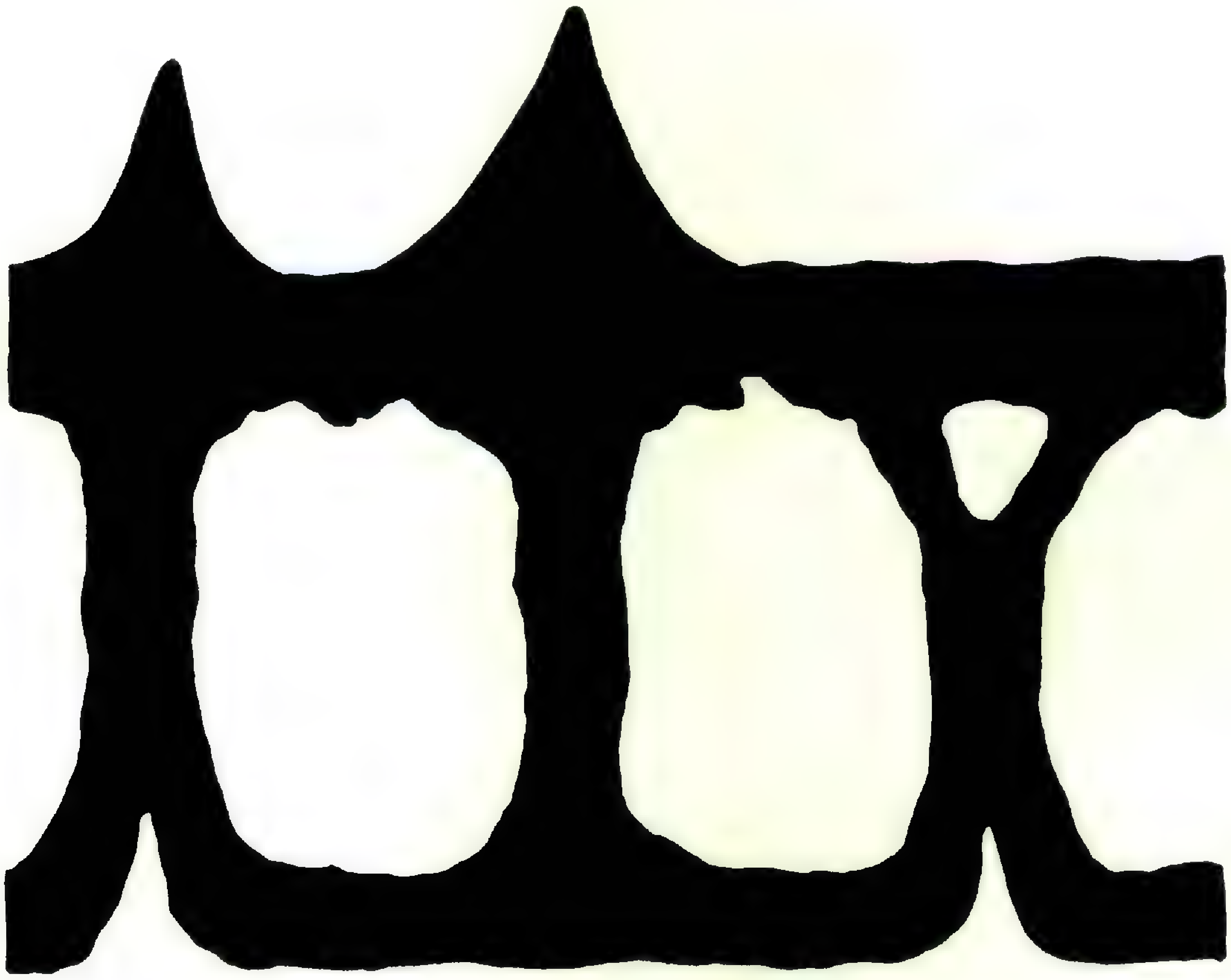


Fig. 5. Forms of solid-single level columellae. (Foot layer and endexine not shown).

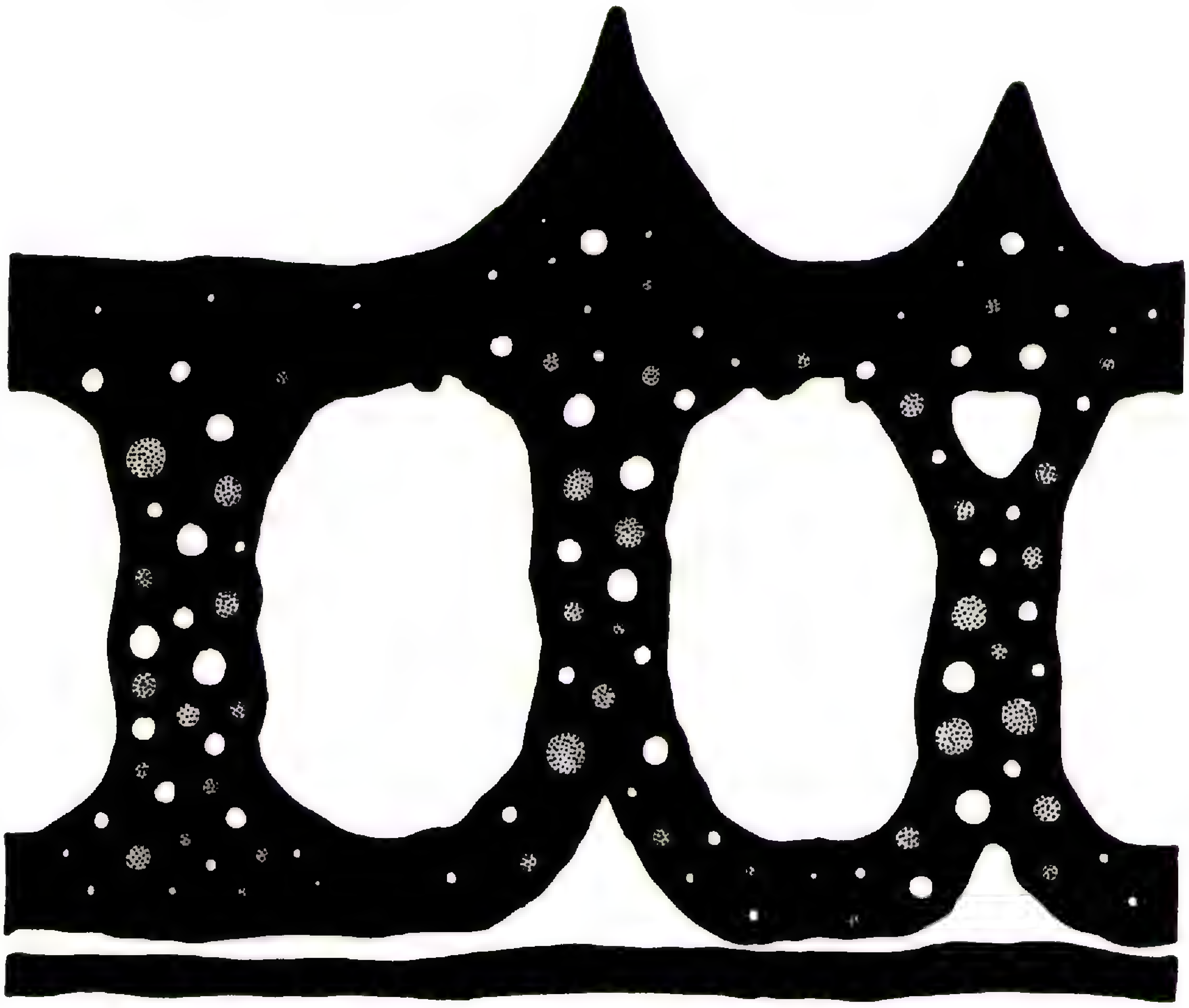


Fig. 6. Internal foramina. Stippling represents precipitated OsO_4 or tapetal debris. Note that the foot layer, separated by a cavus, does not contain internal foramina. (Endexine not shown).

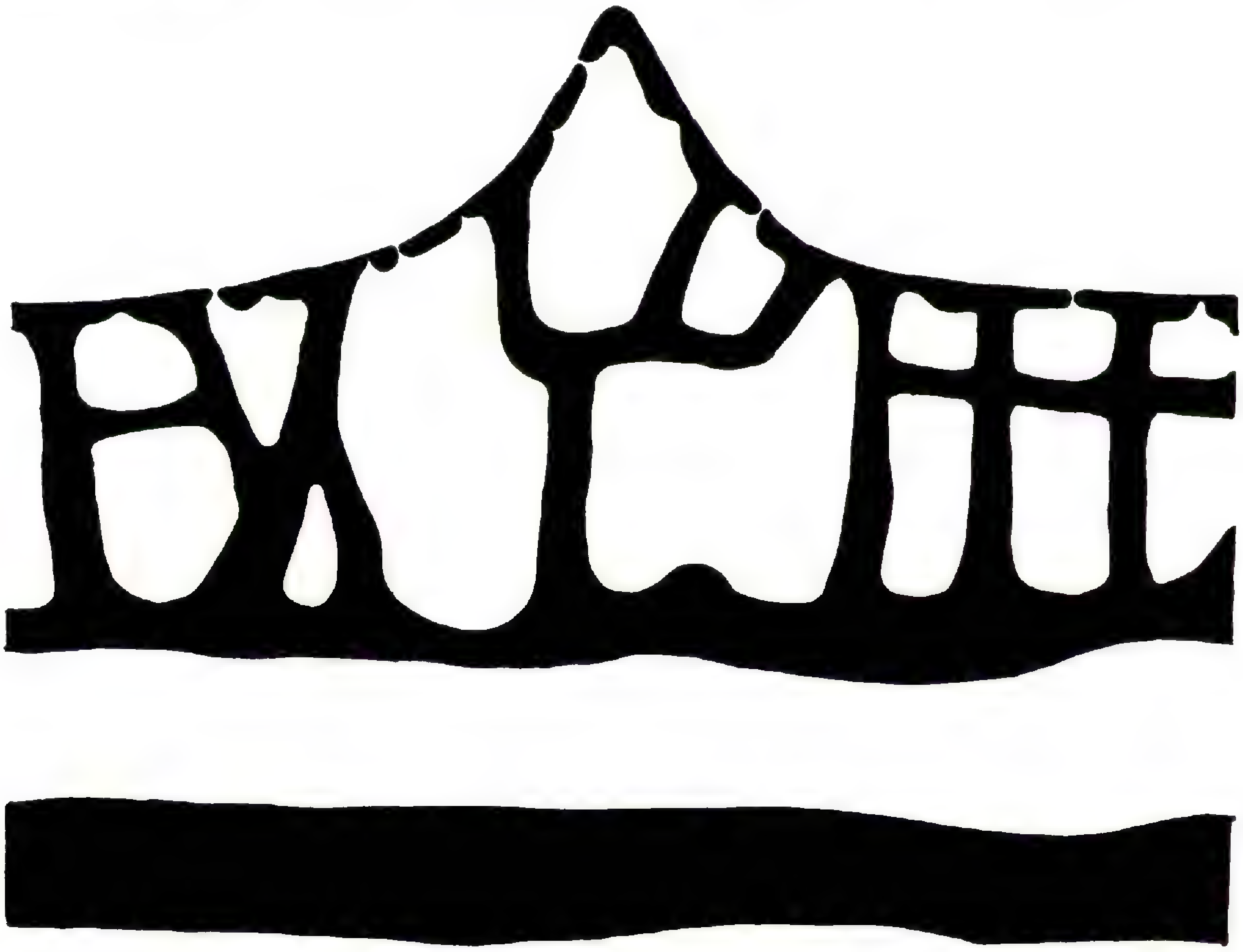


Fig. 7. Forms of internal tecta. At the left the internal tectum is discontinuous; at the right it is continuous. (Endexine not shown).

adjacent, similarly disposed columellae. The horizontal layer (or layers) formed by these lateral branches has been termed "internal tectum" (Skvarla & Larson, 1965a) to distinguish it from the outer, spinule-associated tectum (called the outer or external tectum for the sake of clarity). Both tecta originate from the columellae. Above the area of horizontal branching the columellae again assume a vertical position—the second columellar level—and eventually form the outer tectum. These internal levels are especially useful taxonomic markers. Thus, in the genus *Iva* (discussed below) a complete sequence can be traced which shows pollen walls with sporadic lateral branches (viz. discontinuous internal tectum) in certain species, to a well-defined, continuous internal tectum in more advanced species. Some caution must be exercised when interpreting the discontinuous internal tectum, as it is easy to mistake irregularly arranged columellae as internal tectum units; for this reason numerous different sectional views must be analyzed before one can be sure of a correct interpretation. Double level columellae are present in caveate as well as non-caveate exines.

(4) *Solid, multiple-level columellae.* The columellae in this class differ from those in the preceding one in that additional levels of internal tecta with corresponding columellae occur above the basic columellar—internal tectum level. In some species the number of levels can be discerned readily while in other taxa the patterns are intricately arranged in delicate mosaics and nets which defy ready placement. Columellae of this type are presently found only in non-caveate exines.

Tectum. The tectum, formed by expanded distal portions of the columellae, has been considered in the above discussion from most of its important aspects. Supplementary remarks relate to the internal foramina, the continuity of the tectum, and the spinules. In regard to the internal foramina, a positive relationship exists between the columellae and tectum: exines have not been observed with internal foramina restricted to only one of these units. However, as noted in the *Heliantheae* (Skvarla & Larson, 1965a), the number and diameter of the internal foramina decrease toward the outer margins of the tectum with only vestiges remaining in the spinules. Our work with additional tribes now extends this observation to all taxa possessing internal foramina.

In an individual pollen grain the tectum usually exhibits both continuous (imperforate) and discontinuous (perforate) characters. This rather consistent morphological feature negates tectum unity or disunity as a taxonomic marker.

Tectum spinules. In addition to spinule length and degree of acuity, characters best observed by light microscopy, and the above-mentioned internal foramina, other morphological variations have been noted. These variations center about two classes of openings which perpendicularly transect the long axis of the spinule: the first class is located in the spinule base; the second class is located a short distance below the spinule tip. In a previous study (Skvarla & Larson, 1965a), a basally located opening was recognized in exine spinules in the *Heliantheae* and *Anthemideae*, and was interpreted as representing a channel formed by columellar and tecta fusions. With our present study it is apparent that columellae and tectum construction can form spinules having several basal channels or even large gaps

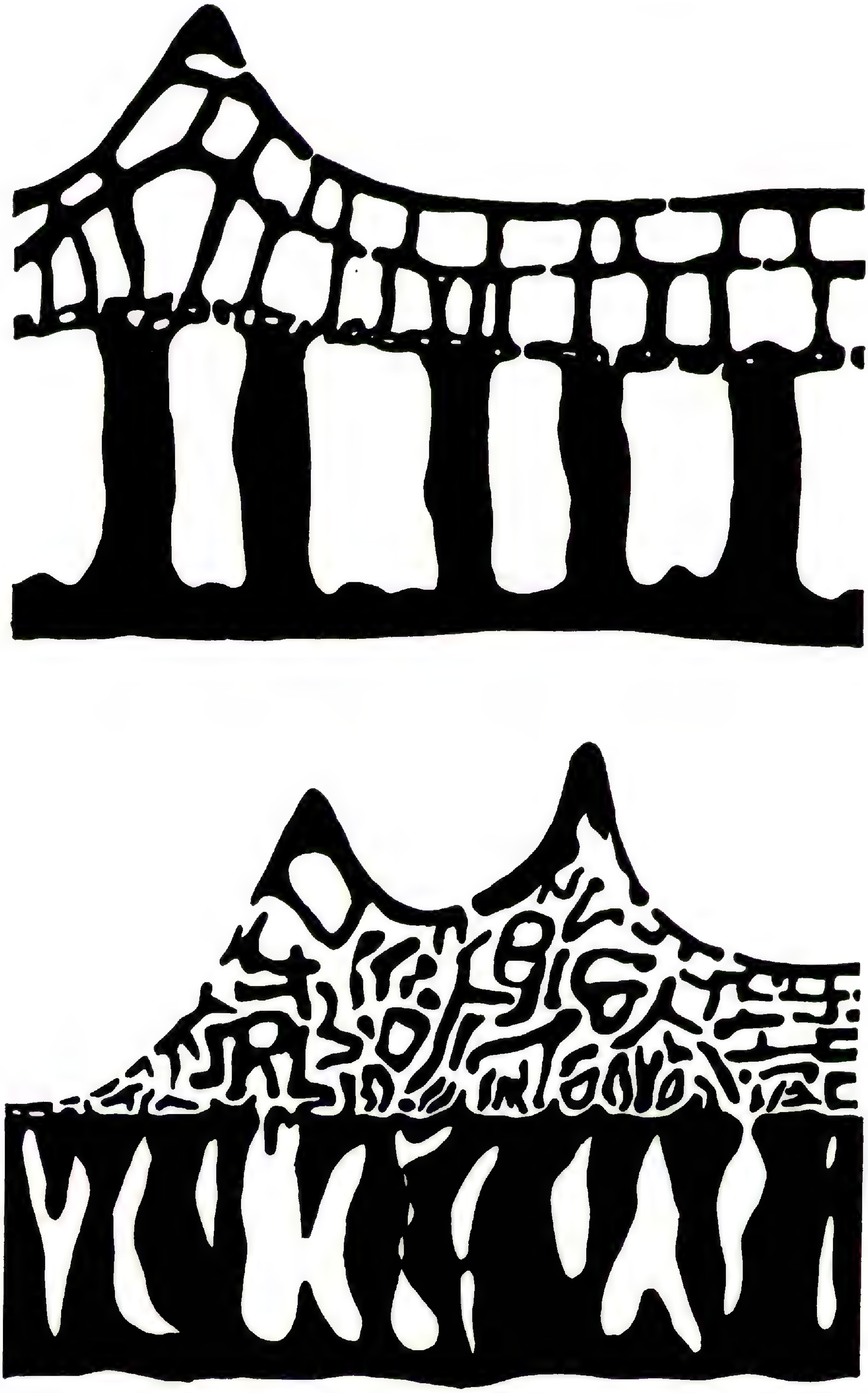


Fig. 8. Multiple-level columellar patterns. Fig. 8A (top) shows two internal tecta levels with corresponding columellae. In Fig. 8B (bottom) the internal tecta-columellar relationship is complex above the first columellar level. (Endexine not shown).

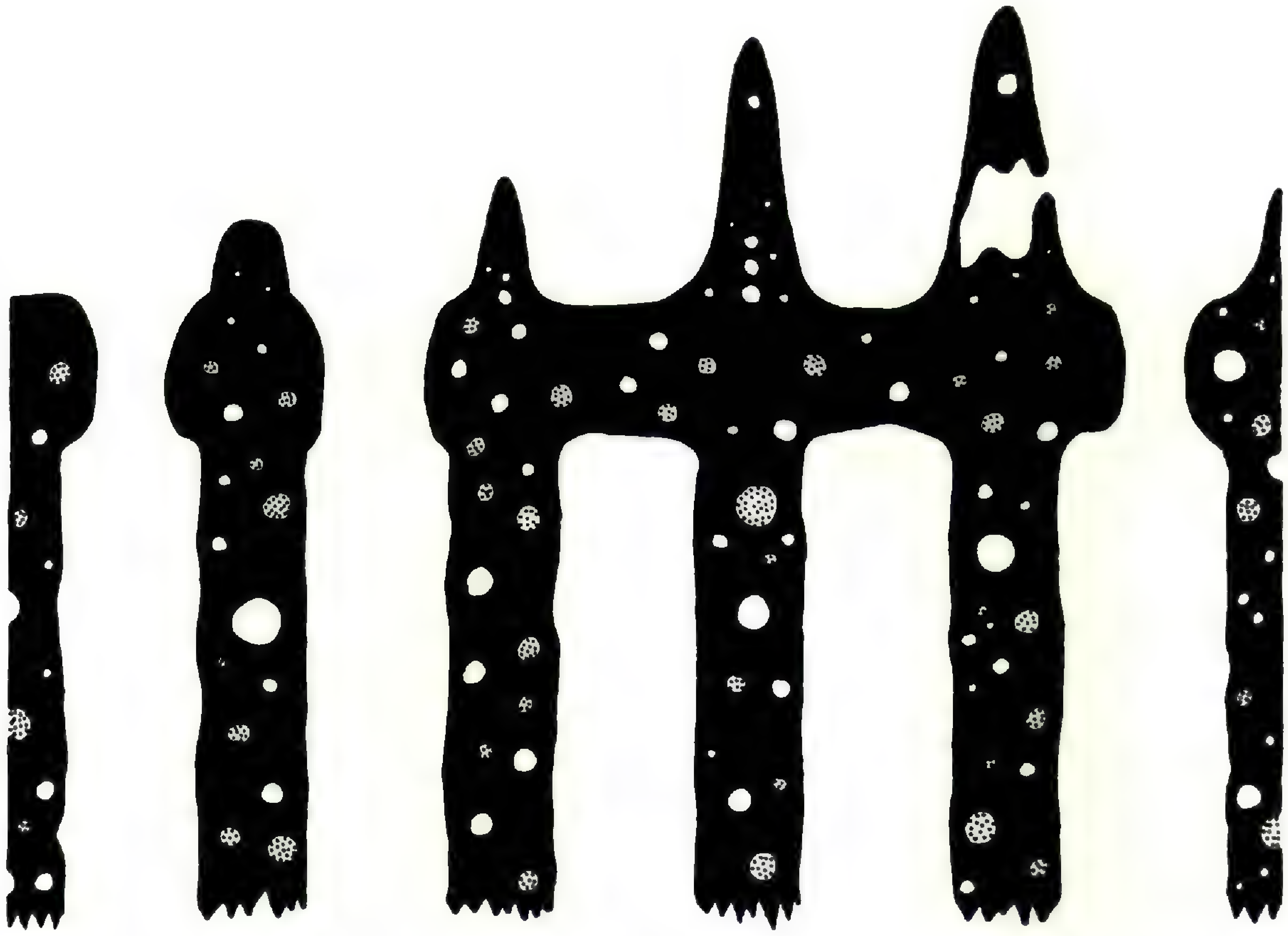


Fig. 9. Tectum-spinule characters. Spine at right shows basal gap and subapical channel. Adjacent spine (immediately to the left) shows a subapical channel and three basal channels surrounded by minute internal foramina. Internal foramina with larger diameters are common throughout columellae and tectum.

On the other hand, the more apically located opening does not appear to bear the same morphological relationship with the tectum and columellae as the basal opening. In the absence of developmental studies, we can only note that subapical channels appear to be a common feature of most spinules, and therefore, are not expected to have taxonomic relevance.

Pollen Wall Morphology at Tribal Level

With the preceding serving as an introduction to the ultrastructural morphology of the pollen wall, we shall now discuss the systematic implications of these data. Characteristics of the pollen wall layers for the various tribes will be listed and specific taxa discussed when pertinent. A short commentary will also be included on the work of other investigators in an attempt to evaluate their ideas and interpretations against those of our own. The number of species examined under some of the tribes hardly justifies an attempt at this time to make tribal circumscription on an ultrastructural basis, and we wish to make it clear that the purpose of including such observations is to present a more comprehensive account of the *Compositae* pollen wall in general and of what might be anticipated in our future studies.

1. Vernonieae (Fig. 10, 11).

In *Vernonia pacchensis,* the endexine is thick (endexine-foot layer ratio approximately 3: 1), slightly lamellate and has a smooth lower surface. In some sectional views the endexine shows a pronounced doming beneath columellar areas (Fig. 11). The foot layer is thin and increases only slightly in thickness at columellar junctions. Continuous with the foot layer are thick columellae which digitate to form an echinolopholate[4] ektexine characterized by a perforate tectum and sharp spinules. The spinules contain a basal channel. In lacunar[5] areas the tectum is not supported by columellae.

Pollen of *V. pacchensis* agrees with the "*Lychnophora—Typ.*" of Stix (1960) and reinforces the endexine-foot layer relationship apparently questioned by her, but disagrees with her "*Vernonia—Typ.*" as well as with her diagram of *V. scorpioides* (Plate II, Fig. A) with regard to columellar and tectum characteristics.

The *Vernonieae* hold much promise for future electron microscopic investigations. Stix has indicated at least three different pollen types while Wodehouse (1928b) has used *Vernonia* to illustrate the phylogenetic value of pollen characters. Cronquist (1955) has suggested a megamorphic relationship with the *Cynareae* and *Mutiseae,* and it is possible that a more intensive electron microscopic survey will point to yet other evolutionary alignments.

2. Astereae (Fig. 12).

The species of this tribe have proved to be remarkably uniform as viewed from electron microscopic work on their pollen walls. Their ultrastructure is like that of the *Heliantheae;* therefore, we have described them as possessing a Helianthoid pattern (to be discussed), presumably reflecting an evolutionary relationship with that tribe.

3. Inuleae (Fig. 13, 14, 15).

The ultrastructural morphologies of *Anaphalis margaritacea* (Fig. 13), *Craspedia richea* (Fig. 14), and *Dimeresia howelli* are similar to the *Heliantheae* and are tentatively considered as having a Helianthoid pattern. *Inula britannica* (Fig. 15), on the other hand, has a different wall morphology. The endexine is approximately 3 to 4 times the thickness of the foot layer and is highly disrupted along the lower surface. The foot layer is of uniform thickness and is separated from the columellae by a cavus. Above the cavus, the single level columellae display thickened and intermittently connected bases. The tectum is thin and perforate. Internal foramina are absent. Long, blunt spinules are common and characterized by a single distal channel. The columellae and tectum forming the base of the spinules are complex and indicate a multi-columellar level. In the above characters, *I. britannica* more closely resembles the Senecioid pattern (to be discussed); however, our present sampling is too limited to do anything more than make cursory observations.

[4] Ridges bearing spines, according to Wodehouse (1928b).

[5] Depressed areas between ridges, according to Wodehouse (1928b).

4. HELIANTHEAE (Fig. 16, 17, 18).

The taxa listed on page 000 represent a sampling from the subtribes *Lagascinae, Melampodinae, Zinninae, Verbesininae, Coreopsidinae, Galinsoginae* and *Madinae.* The internal morphology of the pollen wall is as follows:

Endexine. Of uniform intrinsic thickness in all species examined; foot layer-endexine ratios at least 1: 3, occasionally greater but never less. Commonly highly lamellate in colpial and intercolpial areas. Disrupted lower surfaces common to many, but not all taxa.

Ektexine and Cavea.

(a) *Foot layer*: very thin in all species, in some instances difficult to observe without proper staining techniques. Basal lamellations interbed with endexine in *Argyroxiphium virescens, Galinsoga ciliata, Bebbia juncea* (these three species were also studied by Skvarla & Larson, 1965b), *Melampodium leucathemum, Zinnia angustifolia, Viquiera dentata, Baldwinia uniflora* and *Cosmos bipinnatus.* Domed areas are present beneath caveate regions of spinules in many species.

(b) *Cavea*: present without exception in all species.

(c) *Columellae*: of nearly equal length in all species and with basally fused regions (i.e. lower parts of columellae immediately above cavea) equal or occasionally exceeding thickness of tectum (i.e. upper parts of columellae). Internal foramina common to all species.

(d) *Tectum*: commonly varies from continuous to discontinuous in individual taxa. Internal foramina as common as in columellae. Spinule lengths highly variable (best determined by light microscopy) and always containing at least a single basal channel, and sometimes a subapical channel (Fig. 16).

Because of the uniform ultrastructural morphology noted in species of the *Heliantheae*, we have designated this type of pollen wall pattern as the Helianthoid type. The only exception to the Helianthoid pattern so far noted is that found in *Parthenice mollis.* As discussed in an earlier paper (Skvarla & Larson, 1965a), *Parthenice* can be distinguished by columellar complexity in the form of a loose, discontinuous internal tectum and in lacking internal foramina. The difference in ultrastructural morphology from other taxa in the *Heliantheae* is particularly significant in view of its curious taxonomic position. *P. mollis,* on megamorphic features, was placed in the subtribe *Melampodinae* by Bentham (1873). However, Wodehouse (1928a) considered the species to be the prototype for the *Ambrosia* group *(Ambrosieae)* generally. Electron microscopy does not corroborate Wodehouse's proposal but rather suggests that *P. mollis* might be the prototype for only certain members of the *Ambrosia* group.

An alternative to Wodehouse's suggestion is that of Bentham (1873). In discussing the *Ambrosieae* he states that the group is ". . . without doubt connected with *Artemisia* [tribe *Anthemideae*], as well as with *Melampodineae* [tribe *Heliantheae*], having much of the habit of the former and passing into the latter through *Parthenice;* but geographically, as well as structurally, the relationship to *Melampodineae* appears to me to be closest" (p. 435).

Obviously, *Parthenice* is not an easy genus to place and it might be that the genus, phyletically speaking, stands somewhere within the aggregate triangle, *Heliantheae—Ambrosieae—Anthemideae*. Still, Bentham (1873 p. 436) felt that *Parthenice* was "too closely allied to *Parthenium* to be widely separated from it . . .", an interesting observation, for *Parthenium* possesses pollen characters which appear to tie in with those taxa of the *Ambrosieae* not related to *Parthenice mollis*.

5. Ambrosieae (Fig. 19, 20).

We have found the internal structures of *Ambrosieae* to be extremely variable, and this variation has been discussed in detail by Skvarla & Larson (1965a). Therefore, we will only briefly review these data here. In the descriptions that follow, we have grouped the taxon according to the phyletic sequence proposed by Wodehouse (1928a, 1935).

Oxytenia acerosa (=*Iva acerosa*) and *Chorisiva nevadensis* (=*Iva nevadensis*): exine is typically of the Helianthoid pollen type. *Dicoria canescens* and *D. brandegeii*: the exines differ from *O. acerosa* in that the columellae are devoid of internal foramina. *Cyclachaena* (=*Iva xanthifolia; I. ambrosiaefolia* and two subspecies): the four taxa examined by us showed two variations in morphological organizations. *I. xanthifolia* is similar to *Dicoria; I. ambrosiaefolia* and subspecies are characterized by a discontinuous internal tectum and in lacking internal foramina, features which favor a relationship to *Parthenice mollis*. *Euphrosyne parthenifolia* and *Leuciva* (=*I. dealbata*): typical Helianthoid type pattern.

The genus *Iva* has been of particular interest because of the intensive study of pollen morphology given it by Wodehouse (1928a), and more recently by Jackson (1960). The latter incorporated morphological and cytotaxonomical information along with a light microscopic surface description of the pollen. Briefly Jackson divided *Iva* into 3 sections:

(1) Section *Linearbractea*: *I. microcephala, I. asperifolia, I. angustifolia* and *I. texensis*. This section exhibited uniform ultrastructural morphology. All exines are caveate, have a single well-defined internal tectum and are wanting in internal foramina.

(2) Section *Iva*: *I. annua* (+ 3 subspecies), *I. imbricata, I. fructescens* (+ 2 subspecies), *I. cheiranthifolia, I. hayesiana,* and *I. axillaris*. A slight heterogeneity is noted in that *I. axillaris* displayed a weakly formed, discontinuous, internal tectum while the other species in this section were nearly identical to *Linearbractea*.

(3) Section *Cyclachaena*: *I. acerosa, I. dealbata, I. nevadensis, I. xanthifolia* and *I. ambrosiaefolia* (+ 2 subspecies). Considerable ultrastructural diversity can be seen in this section. *I. acerosa, I. dealbata* and *I. nevadensis* exhibit Helianthoid pollen; *I. xanthifolia* differs from the preceding species by lacking internal foramina; *I. ambrosiaefolia* (and subspecies) is similar to *I. axillaris* in containing an internal tectum.

These data suggest several different pollen morphological trends in the *Ambrosieae* (Skvarla & Larson, 1965a). One such series, based on the progressive

strengthening of the internal tectum (all other exine features being essentially equal), started with the discontinuous internal tectum of *Parthenice mollis*, included similarly constructed *Iva* species and terminated with *Iva* species having a strongly pronounced internal tectum. The taxa in this series were referred to as the ivoid palynological section. A second series using the same characters was given for *Xanthium*, with *X. spinosum* considered to be the prototype. While these two palynological sections were considered as having a parallel evolution it would also be possible, at least on ultrastructural grounds, to relate *Xanthium* species to the ivoid palynological section. Another series, termed the ambrosoid palynological section, relates part of the *Ambrosia* group through *Parthenium* (rather than *Parthenice*) of the *Melampodinae* to include *Oxytenia, Dicoria, Euphrosyne,* several species of section *Cyclachaena* of the genus *Iva, Hymenoclea,* and culminating with *Ambrosia* (including *Franseria*).

These series, as emphasized by Skvarla & Larson, are not believed to be phyletic; they are based strictly on ultrastructural characters of the pollen wall. However, in some instances phyletic interpretations do seem tenable. For example, internal foramina have not been observed in the supposedly advanced taxa of any of the three palynological sections (with the exception of their questionable existence in *Xanthium*) and it is quite possible that internal foramina are a primitive character. It will be recalled that internal foramina are characteristic of the *Heliantheae*, the tribe which is generally considered as the most primitive in the *Compositae*.

It is apparent that the *Ambrosieae* possess pollen types which contrast with the homogeneous ultrastructural pattern found for the *Heliantheae* generally. Thus the pollen evidence supports the treatment of this group as a separate tribe. We should like to stress, however, that taxonomic displacements and rearrangements cannot be made exclusively on the basis of pollen ultrastructural differences since, as will be subsequently demonstrated, there are tribes in the *Compositae* which possess heterogeneous pollen wall types. In the case of the *Ambrosieae*, however, the lucid and convincing evidence presented by Payne (1963, 1964) and Payne et al. (1964), and the data of the present authors suggest recognition as a tribe. The disagreements with some of Payne's conclusions (Skvarla & Larson, 1965a) were principally with respect to the interpretation of the pollen wall morphology, points which have now been mutually resolved.

Concerning an ancestral group for the *Ambrosieae* we can add nothing more at this time to what has been presented already, other than to suggest that while the relationship is close to the *Heliantheae* it may actually occupy a position intermediate between the *Heliantheae* and *Anthemideae*. A joint project between Dr. Payne and the senior author is being initiated to further resolve this question.

6. HELENIEAE (Fig. 21, 22, 23, 24, 25, 26).

With the exception of *Cacosmia rugosa, Amblyopappus pusillus* and the genus *Blennosperma* (p. 238), the pollen wall morphology of this tribe is essentially of the Helianthoid type. The close resemblance of pollen walls in the *Heliantheae*

and the *Helenieae* underscores the suggestion by several taxonomists (Leonhardt, 1949; Turner, 1956; Cronquist, 1955) that the affinities of most of the taxa in this tribe lie with the *Heliantheae.*

The tribal position of *Cacosmia, Amblyopappus* and *Blennosperma* has been questioned on morphological grounds by the junior author and the present ultrastructural picture apparently substantiates this judgment. The pollen wall morphology of these genera is as follows:

(1) *Cacosmia rugosa* var. *arachnoides* (Fig. 21, 22): endexine thickness about 4-5 times that of the foot layer. The lower endexine surface is mainly smooth and only occasionally displays disrupted areas. Indigenous lamellations are confined to the upper region of the endexine and are remarkably concentrated in the colpus (Fig. 22). Associated with these lamellae are gaps or holes. The foot layer is of variable thickness and displays tightly concentrated lamellar microfibrils near its base. These microfibrils do not appear to penetrate the endexine. Broad columellae are basally continuous with the foot layer. Distally the columellae are branched to form a continuous internal tectum. In areas away from columellar support the internal tectum appears somewhat collapsed and approaches, but never reaches, the foot layer. Short levels of columellae protrude upward from the internal tectum and at their termini unite to form the outer tectum. Blunt spinules commonly contain single, basally positioned channels.

Superficially, the pollen morphology of *Cacosmia* is similar to that found in the *Anthemideae.* However, the fewer and thicker columellae, the collapsed nature of the ektexine, the large endexine-foot layer ratio, and the complicated endexine do not favor its inclusion there. Additionally, the completely different ultrastructural organization from *Calea* pollen (*Heliantheae*) does not agree with the suggested megamorphic relationship of *Cacosmia* with the latter (Cronquist, 1955). Present evidence would favor the placement of *Cacosmia* in the *Liabinae* of the *Senecioneae,* a position which seems valid on both micro- and megamorphic grounds.

(2) *Amblyopappus pusillus* (Fig. 23): differs from the Helianthoid pattern primarily in lacking internal foramina and secondarily by a highly lamellate endexine as well as disrupted lower endexine surfaces. In these characters it appears to be more similar to the *Senecioneae,* and in light of other evidence (Turner, unpublished), it might best be placed in this tribe.

(3) *Blennosperma*: The systematic position of *Blennosperma* had been questioned on morphological and cytotaxonomical grounds by several workers (Turner, 1956; Ornduff, 1963, 1964). Our electron microscopic work has shown that *Blennosperma,* with a highly disrupted endexine, a foot layer-endexine ratio of 1:3, a domed foot layer under the spinule regions, caveate ektexine, and solid, single level columellae, appears identical to *Crocidium* in the *Senecioneae,* and we have accordingly removed *Blennosperma* from the *Helenieae* and placed it next to *Crocidium* (Skvarla & Turner, 1966).

7. ANTHEMIDEAE (Fig. 27, 28).

The *Anthemideae* are characterized by essentially uniform pollen ultrastructure (Skvarla & Larson, 1965a) as follows:

Endexine: Of uniform intrinsic thickness and considerably thicker in comparison to other tribes. Endexine-foot layer ratio approximately 1: 1. Usually not as lamellate as in other tribes nor with appreciable disrupted lower surfaces.

Ektexine.

(a) *Foot layer:* well thickened and easily observed. Basal lamellae have not been seen so far.

(b) *Cavea:* not present in any species.

(c) *Columellae:* complex in nature. They are generally thickened and lack internal foramina (internal foramina are not present in any ektexine unit). The columellae typically digitate and form from one to several complex levels of internal tecta. Only in the numbers of these levels for various taxa has any ultrastructural variation been observed. On this basis the following groupings can be made.

(1) *Single internal tectum: Tanacetum camphoratum, Leucanthemum vulgare, L. gussonii, Aaronsohnia factorovsky, Anthemis arvensis, A. micheliana, A. paranassica, A. ruthenica, A. tinctoria.*

(2) *Two internal tectum levels: Anthemis cotula, Chrysanthemum maximum, Crossostephium turkestanicum, Tanacetum parthenium.*

(3) *More than two internal tectum levels: Achillea lanulosa, Artemisia absinthium, A. annua, A. arbuscula, A. cana, Matricaria chamomilla.*

(d) *Tectum (outer):* for most species the tectum is essentially continuous but with local perforations. Spinule lengths, as discussed by Wodehouse (1926, 1935), are highly variable.

8. SENECIONEAE (Fig. 29, 30, 31).

Since many of the species listed for the *Senecioneae* (p. 000) have been extensively described in a previous paper (Skvarla & Turner, 1966), we will omit specific ultrastructural descriptions and confine our discussion to generalized observations. We have recognized three ultrastructural pollen wall patterns in this tribe: (1) a Helianthoid pattern, (2) a Senecioid pattern similar to the Helianthoid type but lacking internal foramina, (3) a pattern somewhat similar to that found in the *Anthemideae* and tentatively considered as the "Anthemoid-like" pattern.

The Helianthoid pattern is found in *Bartlettia, Gynoxys, Haploesthes, Arnica, Tetradymia, Cacalia, Crassocephalum, Cineraria, Lepidospartum, Schistocarpha* and *Senecio glabellus.* The Senecioid pattern was observed in *Blennosperma, Crocidium, Emilia, Euryops, Gynura, Petasites, Peucephyllum, Werneria,* and all species of *Senecio* except *S. glabellus.* The "Anthemoid-like" pattern occurs in *Liabum* and *Sinclaria.* Of the two species of *Liabum* examined, both possess foot layer microfibrils similar to those observed in *Cacosmia.* Additionally, other ultrastructural characters of *Liabum* (viz. columellae, tectum etc.) are identical with *Cacosmia.*

In our discussion of the *Heliantheae* and *Ambrosieae*, we cautioned against removal of taxa from tribes solely on the basis of divergent pollen types. Thus, the very large and natural genus *Senecio* with only six species examined to date is seen to possess at least two quite different pollen types: *S. glabellus* with a Helianthoid morphology and the remaining five with Senecioid morphologies. The term Senecioid pollen type for those species lacking internal foramina is adopted out of convenience for it is clear that more than one pollen type can be expected for the tribe, and the preponderance of one type over another can only be guessed at with our present meagre sample.

9. Arctotideae (Fig. 32, 33).

The pollen walls of *Arctotis stoechdifolia* and *Didelta* (Fig. 32) are different from *Berkheopsis diffusa*. In the former two taxa the endexine is variable in thickness, slightly lamellate, and with occasionally disrupted lower surfaces. The foot layer is thin to the point of being scarcely perceptible; the foot layer-endexine ratio is approximately 1:5. Cavea separate the remainder of the ektexine from the foot layer. Basally, the columellae are conspicuously conjunct; distally, the columellae form a perforate tectum. Blunt spinules are characterized by large basal gaps.

In *Berkheopsis diffusa* (Fig. 33) the endexine is thick, lamellate, and has fairly uniform lower surfaces. The foot layer is extremely thin with a 1:5 thickness ratio with the endexine. *Berkheopsis* is best distinguished from *Arctotis* and *Didelta* by the complexity of the caveate portion of the ektexine. Here, a lopholate ektexine is formed by complex patterns of multileveled columellae and internal tecta.

Our description of *A. stoechdifolia* agrees with that of Stix (1960) for the same species for which she uses the term "*Arctotis-Typ.*" However, *Arctotis* seems to agree almost equally well with her "*Berkheya-Typ.*," while our observations on *Berkheopsis* do not agree with this latter type, but rather indicate a superficial similarity to her "*Gazania-Typ.*" or "*Gortheria-Typ.*"

10. Mutisieae (Fig. 34, 35).

The two species examined, *Moquinia volutina* (Fig. 34) and *Mutisia campanulata* (Fig. 35), have different and complex pollen wall morphologies. In *M. volutina*, interpretation of the endexine presents a morphological enigma. The lower ⅓ portion is represented as an electron dense layer of variable thickness and is without lamellate organization. We feel certain that this layer is not a staining artifact because our techniques (viz. osmium stained as well as unstained exines) provided us with corroborating data. In lieu of further study we have designated it simply as endexine-2. The upper ⅔ of the endexine is less electron dense, and contains indigenous lamellae: this layer is designated as endexine-1. The foot layer is uniform in thickness and is continuous with broad columellae. The columellae digitate to form an echinolopholate ektexine, characterized by a thick,

perforate tectum. Long spinules with numerous basally disposed channels are common.

In *Mutisia campanulata,* the endexine also presents difficulties in interpretation. Immediately beneath the foot layer is a zone of tightly packed lamellar tubules (see inset to Fig. 35). Each tubule contains a narrow central core, possibly representing the remnants of intracisternal membrane systems active during pollen wall ontogeny (see discussion by Skvarla & Larson, 1966). The tubules are observed to grade into the overlying foot layer as well as a lower layer (which is interpreted as the endexine) at angles of approximately 20-30°. At the present time it is not possible to interpret this tubular zone adequately. While the endexine and foot layer have been shown to contain indigenous lamellae (as well as exhibiting an intermingling of lamellae of the two layers), tubules of the magnitude and morphological organization as occurs in *Mutisia* have not been observed.

The foot layer in *Mutisia* is continuous with thickened columellae which sharply digitate to form a narrow, fairly continuous internal tectum. Arising from the internal tectum are networks of minute columellar and internal tecta units. Because of the complexity of the ektexine above the first level of thickened columellae, we have not attempted to define these levels from a quantitative standpoint. The external tectum is slightly perforate and forms short spinules.

While we have not seen any ultrastructural pattern which matches that of *Mutisia campanulata,* the lopholate pollen wall of *Moquinia volutina* (with the exception of endexine-2) compares favorably with that of the *Vernonieae.* It is of interest that Wodehouse (1928c, 1929) indicated a *Vernonieae-Mutisieae* relationship through *Barnadesia* of the latter tribe. However, Bentham (1873) felt that the relationships of *Mutiseae* were closer to the *Cynarieae,* a tribe which we have not examined as yet.

Carlquist (1957) suggests that the two-layered ektexine of the *Mutisieae* represents a different and probably advanced type from that of the single layered ektexine in the *Heliantheae* (which is considered to be the more primitive form), a view which the present authors also accept.

11. Cichorieae (Fig. 36, 37).

The ultrastructural morphology of *Pyrrhopappus, Andryala* (Fig. 36), and *Sonchus* (Fig. 37) is similar: the endexine is thick (endexine-foot layer ratio 3: 1), lamellate, and has disrupted lower surfaces. The uniformly thin foot layer is continuous with very thin and short columellae which form an echinolopholate ektexine consisting of 6-7 levels of internal tecta. Away from areas of columellar support (viz. lacunar areas) the number of ektexine levels is reduced to one; in these areas the ektexine appears collapsed. Spinules are long, blunt, and generally contain apical channels.

Of particular interest in the present tribe is the genus *Fitchia.* The external pollen morphology of *Fitchia* was considered similar to the *Heliantheae* (Wodehouse, 1935). The first light microscopic observations on sectioned pollen walls also confirmed this disposition (Carlquist, 1957). Interestingly enough the primary internal feature used to establish the *Heliantheae* relationship was lacunae (=chan-

nels according to our descriptions) at spine bases while cavea apparently were not recognized. Carlquist (1963) examined three additional species which showed a well-developed internal tectum. Although there is little doubt of the *Heliantheae* position of *Fitchia,* it is hoped that ultrastructural studies will furnish us with supplementary data in delineating what was heretofore considered to be a homogeneous tribe.

Concluding Remarks

In bringing this portion of the symposium to a close we would like to comment briefly on future work. In this presentation we have attempted to summarize all of the work of an ultrastructural nature on the pollen wall of the *Compositae.* The data presented, particularly those pertaining to the *Heliantheae, Ambrosieae, Helenieae, Anthemideae* and *Senecioneae,* mostly have been those of the senior author (Skvarla & Larson, 1965a; Skvarla & Larson, 1965b; Skvarla & Turner, 1966). Data acquired more recently have been related to these studies, but it should be obvious that far too little is known about the ultrastructure of the pollen wall of the *Compositae* to draw sweeping phyletic conclusions, particularly as concerns intertribal affinities. Yet sufficient data exist to permit us to state with some confidence that electron microscopic work certainly will help clarify such relationships.

With present sampling we have done little more than scratch the surface in this very large family. While our studies have been limited by our preoccupation with the acetolyzed pollen wall, we would be remiss if we limited our investigations strictly to such materials. We have employed an acetolysis technique rather than using fresh pollen for three reasons: (1) availability of samples; (2) acetolyzing the pollen exines introduces a common denominator which serves to eliminate potential variables; (3) the artificially "fossilized" condition caused by acetolysis leaves the pollen in a favorable state for future electron microscopic paleobotanical comparisons. Although it is believed that the above reasons more than justify the acetolysis technique, information gained from freshly prepared pollen may be just as valuable. The area destroyed by acetolysis, viz. the intine (the callosic-pectinaceous layer interposed between the endexine and plasmalemma) has been given little study by pollen morphologists. The few observations of fresh pollen made by the senior author indicate that intine thickness demonstrates a species-related variation similar to the variations in thickness of the foot layer and endexine observed after acetolysis.

Freshly prepared pollen would also permit examination of the cytoplasmic organelles, etc. While we do not imagine that taxonomic dispositions will be made on the morphological construction of the cytoplasm, we believe that cytoplasmic data, especially as concerns sperm cells, can provide us with supplemental information. The likelihood of taxonomic differentiation at the cytoplasmic level should not be discounted. We have in mind the allergenic species. We feel that allergenic species should be studied for the possible presence of discernible variations in specific groups of organelles. If feasible, antigenic localization at the electron microscopic level would provide a highly sophisticated means of comparing various hayfever species.

Developmental work is another area which should not be neglected. As we have stressed repeatedly in this symposium, developmental work relating to pollen wall formation cannot be minimized since the micro-anatomy can be only arbitrarily defined without such studies. Some of the most cogent studies would be directed toward foot layer lamellae, cavus formation, internal formina formation and organization of multi-level ektexines, and above all, toward the origin of sporopollenin substrates.

Literature Cited

Afzelius, B. M., G. Erdtman & F. Sjöstrand. 1954. On the fine structure of the outer part of the spore wall of *Lycopodium clavatum* as revealed by the electron microscope. Svensk. Bot. Tidskr. **48:** 155-161.

Bentham, G. 1873. Notes on the classification, history, and geographical distribution of *Compositae*. Jour. Linn. Soc. Bot. **13:** 335-557.

Carlquist, S. 1957. The genus *Fitchia* (*Compositae*). Univ. of Calif. Press **29:** 1-144.

———. 1963. Studies in *Fitchia* (*Compositae*): novelties from the Society Islands; anatomical studies. Pacific Science **17:** 282-298.

Chambers, T. C. & H. Godwin. 1961. The fine structure of the pollen wall of *Tilia platyphyllos*. New Phytol. **60:** 393-399.

Cronquist, A. 1955. Phylogeny and taxonomy of the *Compositae*. Amer. Midl. Nat. **53:** 478-511.

Erdtman, G. 1952. Pollen morphology and plant taxonomy. I. Angiosperms. Almquist & Wiksell, Stockholm.

———. 1960. Pollen walls and Angiosperm phylogeny. Bot. Not. **113:** 41-45.

Faegri, K. 1956. Recent trends in palynology. Bot. Rev. **22:** 639-664.

Fernández-Morán, H. & A. O. Dahl. 1952. Electron microscopy of ultrathin frozen sections of pollen grains. Science **116:** 465-467.

Hoffman, O. 1897. *Compositae*, *In* Engler & Prantl, Nat. Pflanzenf. **4:** 87-391.

Iversen, J. & J. Troels-Smith. 1950. Pollenmorfologiske Definitioner og Typer. Danmarks Geol. Unders., 4 rk., **3:** 8.

Jackson, R. C. 1960. A revision of the genus *Iva* L. Univ. Kansas Sci. Bull. **41:** 793-876.

Larson, D. A. & J. J. Skvarla. 1961. The morphology and fine structure of pollen of *Polygala alba* Nutt. and *P. incarnata* L. Pollen et Spores **3:** 21-32.

Leonhardt, R. 1949. Phylogenetisch-systematische Betrachtungen. I. Betrachtungen zur Systematik der Compositen. Oesterr. Bot. Zeitschr. **96:** 293-324.

Mühlethaler, K. 1953. Untersuchungen über die struktur der pollenmembran. Mikroskopie **8:** 103-110.

Ornduff, R. 1963. Experimental studies in two genera of *Helenieae* (*Compositae*): *Blennosperma* and *Lasthenia*. Quart. Rev. Biol. **38:** 141-150.

———. 1964. Biosystematics of *Blennosperma* (*Compositae*). Brittonia **16:** 289-295.

Payne, W. W. 1963. The morphology of the inflorescence of ragweeds (*Ambrosia—Franseria: Compositae*). Amer. Jour. Bot. **50:** 872-880.

———. 1964. A re-evaluation of the genus *Ambrosia* (*Compositae*). Jour. Arnold Arb. **45:** 401-438.

———, P. Raven & D. Kyhos. 1964. Chromosome numbers in *Compositae*. IV *Ambrosieae*. Amer. Jour. Bot. **51:** 419-423.

Rowley, J. R. 1959. The fine structure of the pollen wall in the *Commelinaceae*. Grana Palynologica **2:** 3-30.

———, K. Muhlethaler & A. Frey-Wyssling. 1959. A route for the transfer of materials through the pollen grain wall. Jour. Biophys. Biochem. Cytol. **6:** 537-538.

Skvarla, J. J. 1966. Techniques of pollen and spore electron microscopy. Part I. Staining, dehydration, and embedding. Oklahoma Geology Notes **26:** 179-186.

——— & D. A. Larson. 1965a. An electron microscopic study of pollen morphology in the *Compositae* with special reference to the *Ambrosieae*. Grana Palynologica **6:** 210-269.

———. 1965b. Interbedded exine components in some *Compositae*. Southwest. Nat. **10:** 65-68.

——— & B. L. TURNER. 1966. Pollen wall ultrastucture and its bearing on the systematic position of *Blennosperma* and *Crocidium* (*Compositae*). Amer. Jour. Bot. **53:** 555-562.

———. 1966. Fine structural studies of *Zea mays* pollen. I: cell membranes and exine ontogeny. Amer. Jour. Bot. (in press).

STIX, E. 1960. Pollenmorphologische untersuchungen an Compositen. Grana Palynologica **2:** 41-114.

TURNER, B. L. 1956. A cytotaxonomic study of the genus *Hymenopappus* (*Compositae*). Rhodora **58:** 163-308.

WILSON, L. R. & G. J. GOODMAN. 1963. Techniques of palynology—Part I. Collection and preparation of modern spores and pollen. Okla. Geology Notes **23:** 167-177.

———. 1964. Techniques of palynology—Part II. Microscope-slide preparaton of modern spores and pollen. Okla. Geology Notes **24:** 277-280.

WODEHOUSE, R. P. 1926. Pollen grain morphology in the classification of the *Anthemideae*. Bull. Torrey Bot. Club **53:** 479-485.

———. 1928a. Pollen grains in the identification and classification of plants. I. The *Ambrosiaceae*. loc. cit. **55:** 181-198.

———. 1928b. The phylogenetic value of pollen grain characters. Ann. Bot. **42:** 891-934.

———. 1928c. Pollen grains in the identification and classification of plants, II. *Barnadesia* Bull. Torrey Bot. Club **55:** 449-462.

———. 1929. Pollen grains in the identificaton and classification of plants, IV. The *Mutisieae*. Amer. Jour. Bot. **16:** 297-313.

———. 1935. Pollen Grains. McGraw-Hill, New York.

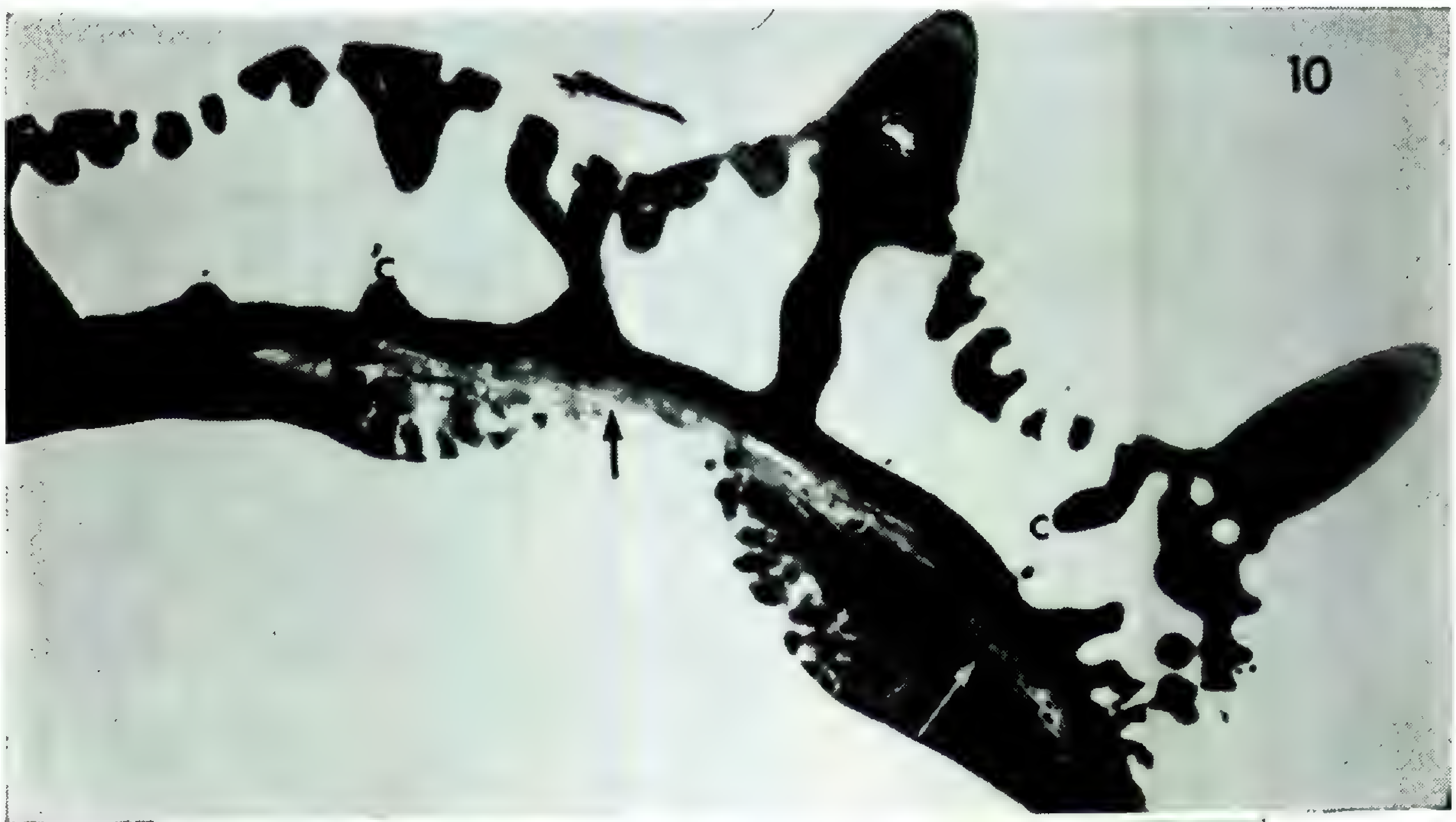
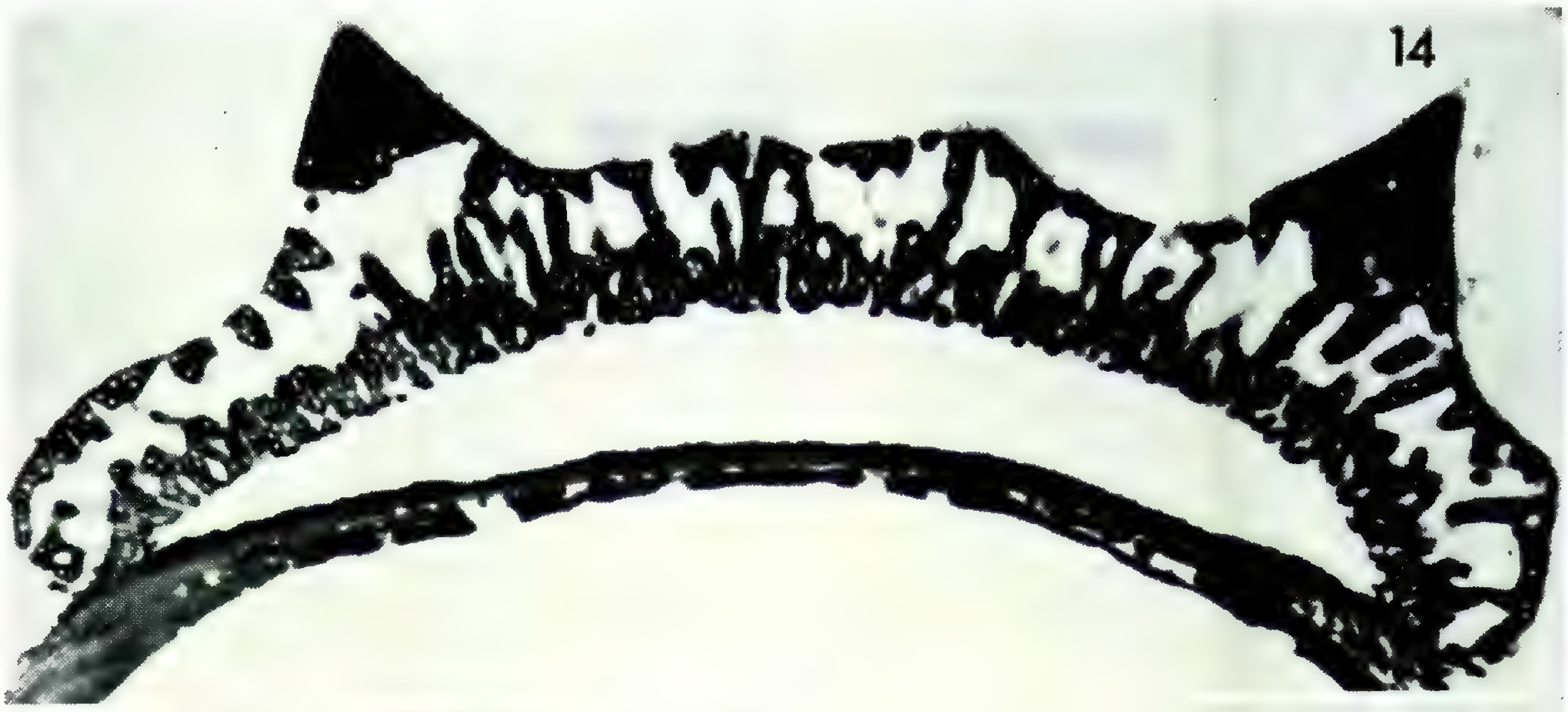


Fig. 10, 11. *Vernonia pacchensis (Vernonieae).* Fig. 10. Section through lopholate area. The endexine contains coarse lamellations (arrows). (The gap in the endexine is result of plane of sectioning passing near germinal aperture.) Columellae (c) appear disconnected from foot layer due to sectioning angle. ca ×6,900. Fig. 11. View illustrating endexine doming beneath columella. ca ×12,000.

Key to Labeling of Electron Micrographs: c—columella, CH·1—basal spinule channel, CH·2—subapical spinule channel, en—endexine, fl—foot layer, G—basal spinule gap, it—internal tectum.

Fig. 12. *Erigeron* sp. *(Astereae)*. Near median-equatorial view. Note internal foramina in ektexine, disrupted lower portion of endexine (arrows) and prominent cavea. ca × 6,000. Fig. 13. *Anaphalis margaritacea* var. *occidentalis (Inuleae)*. The internal foramina in columellae and columellar bases form elongated openings. Note vestiges of internal foramina (arrows) in spinule base. ca × 12,000 (Key to labeling, see Fig. 10).



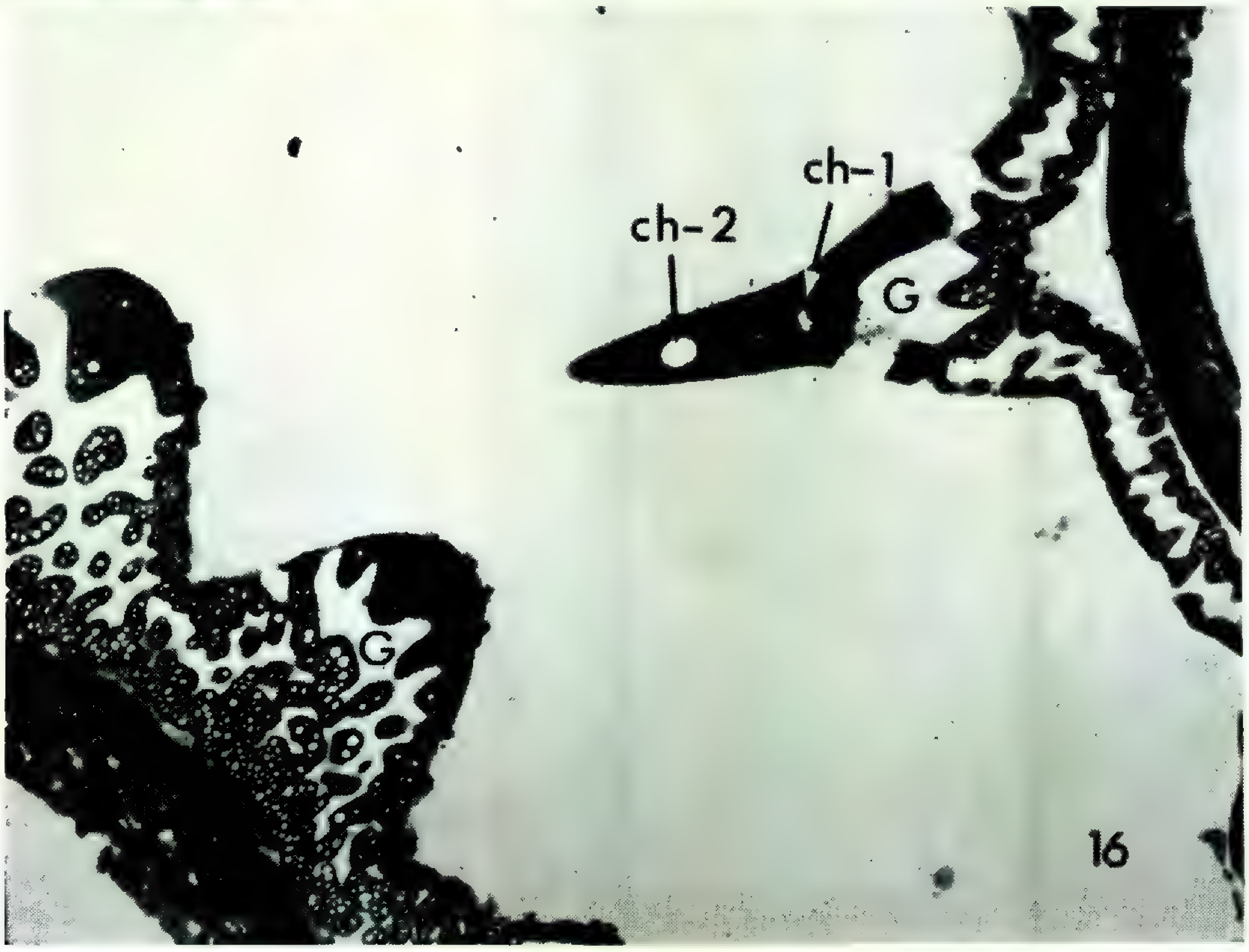
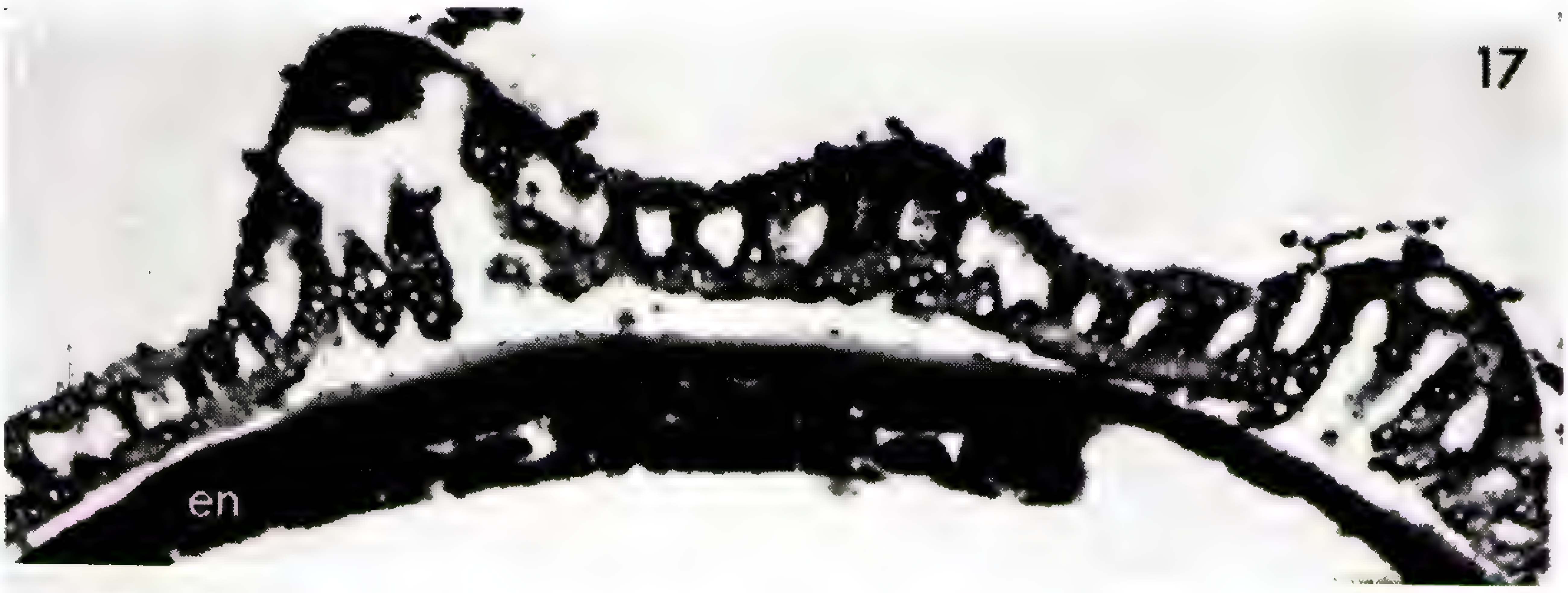
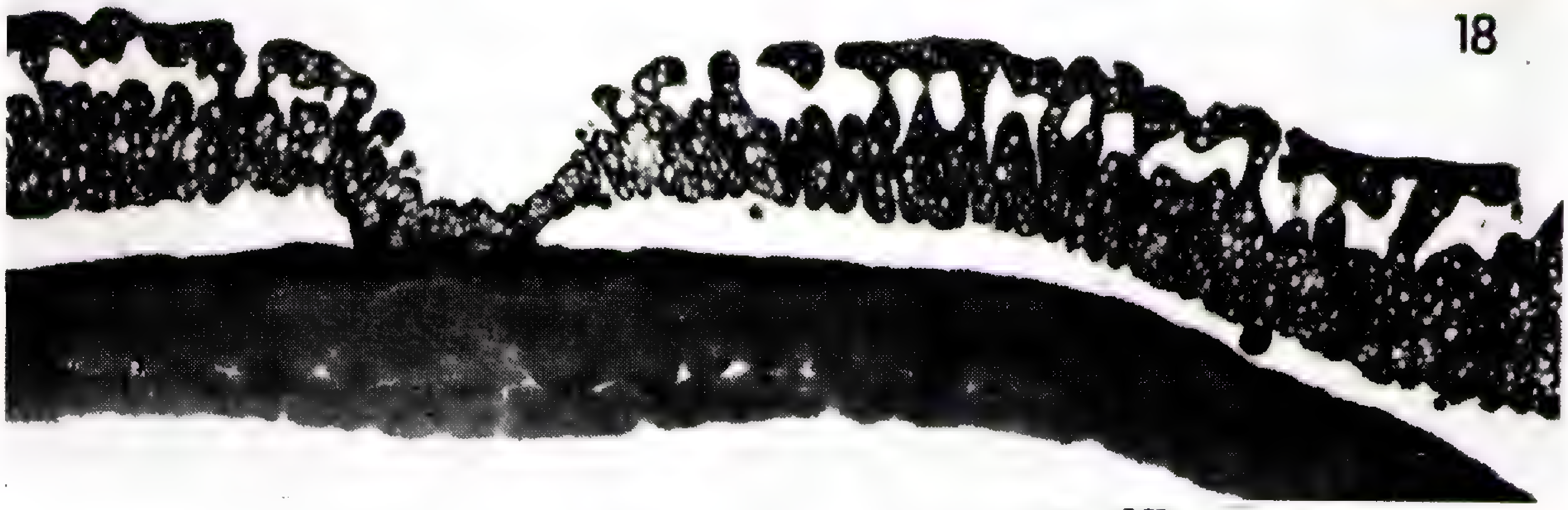


Fig. 14. *Craspedia richea (Inuleae).* The endexine is lamellate and highly disrupted; internal foramina are common but not organized into elongate openings as in Fig. 13. ca ×8,200. Fig. 15. *Inula britannica (Inuleae).* Internal foramina are absent. Beneath spinule area (which is oblique view in this section) the columellae are more complex than in adjacent areas. Note sharp differentiation of ektexine and endexine. ca ×18,000. Fig. 16. *Silphium astericus* (*Heliantheae*). Two different sectional views. Note large gap (G) at spinule bases, basal channel (Ch_1), and subapical channel (Ch_2). The foot layer is clearly differentiated from endexine. ca ×6,200 (Key to labeling, see Fig. 10).





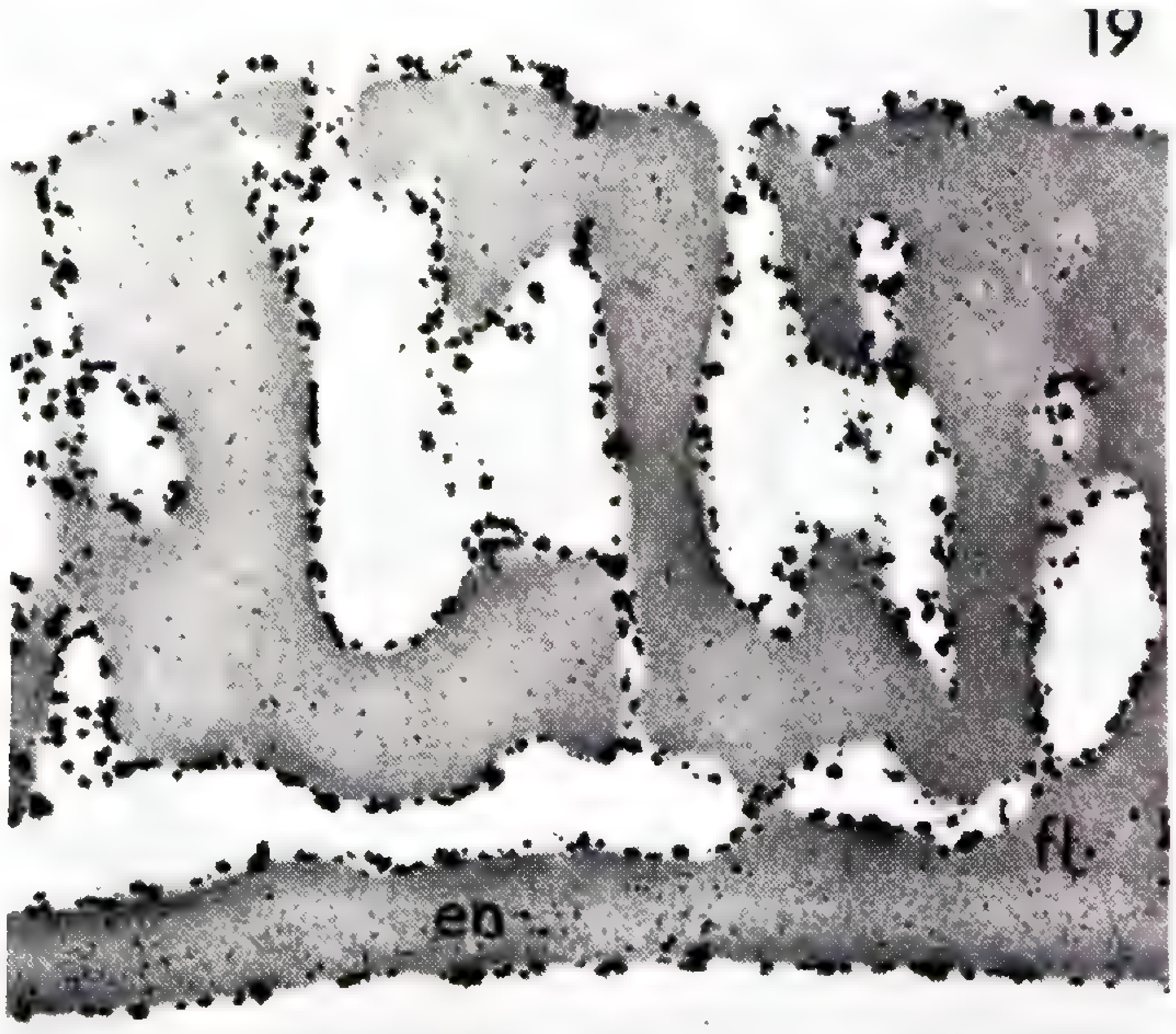


Fig. 17. *Zinnia angustifolia (Heliantheae).* This electron micrograph is included to illustrate that although a "reversal" of exine staining is apparent, the endexine is still sharply differentiated from the ektexine. ca ×10,500. Fig. 18. *Marshallia caespitosa (Heliantheae).* Section through colpus. Note decrease in columellar dimensions and fusion with the foot layer. ca ×8,000. Fig. 19. *Hymenoclea fasciculata (Ambrosieae).* Near polar view. Note union of columellar base with foot layer (at extreme right). The black dots surrounding the exine represent osmium precipitate. ca ×47,500. Fig. 20. *Iva annua* var. *annua (Ambrosieae).* Near polar view. A loose, intermittent internal tectum is formed by the columellae. Note occasional attachment of columellae with foot layer. ca ×30,000 (Key to labeling, see Fig. 10).

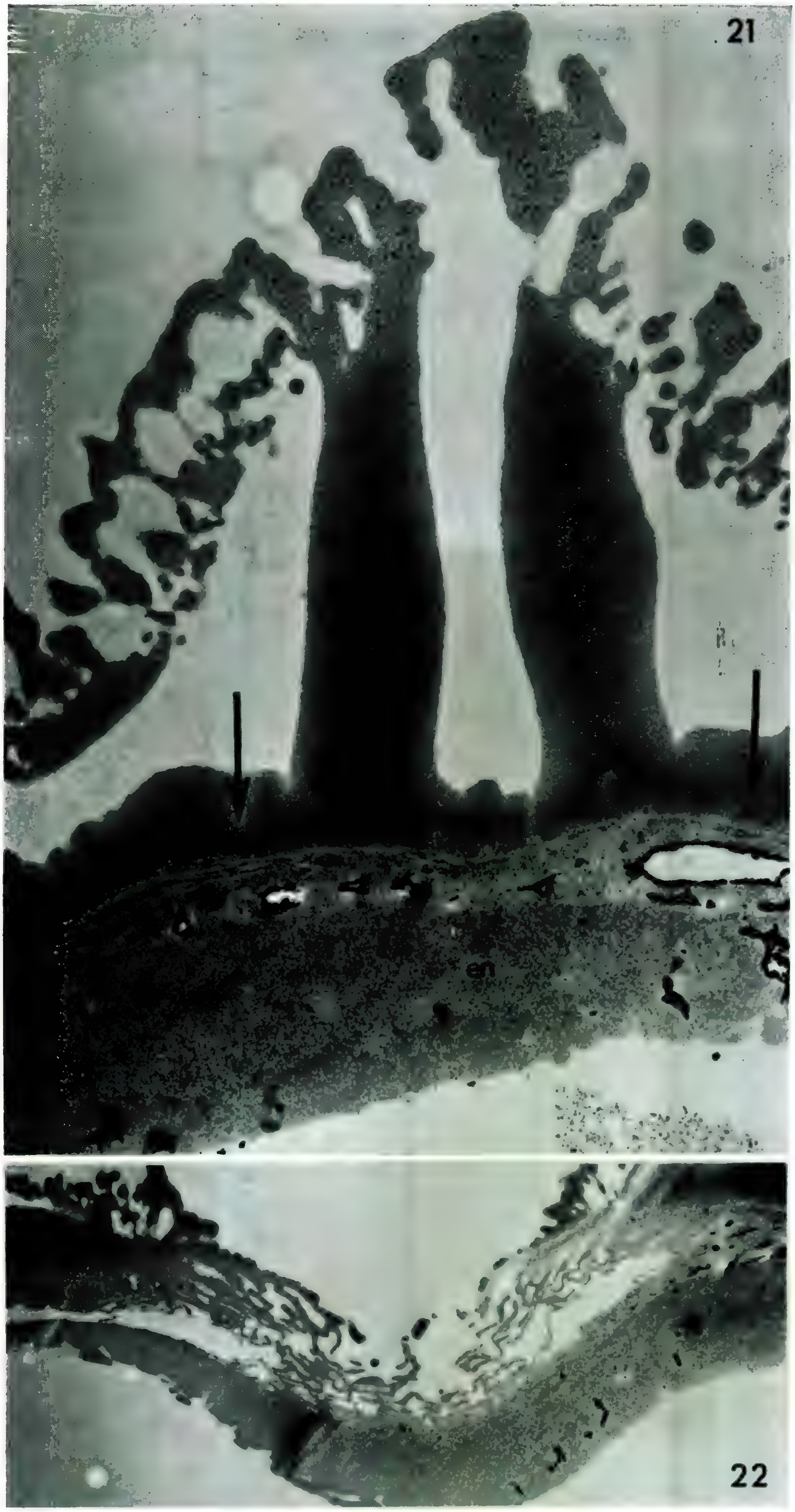
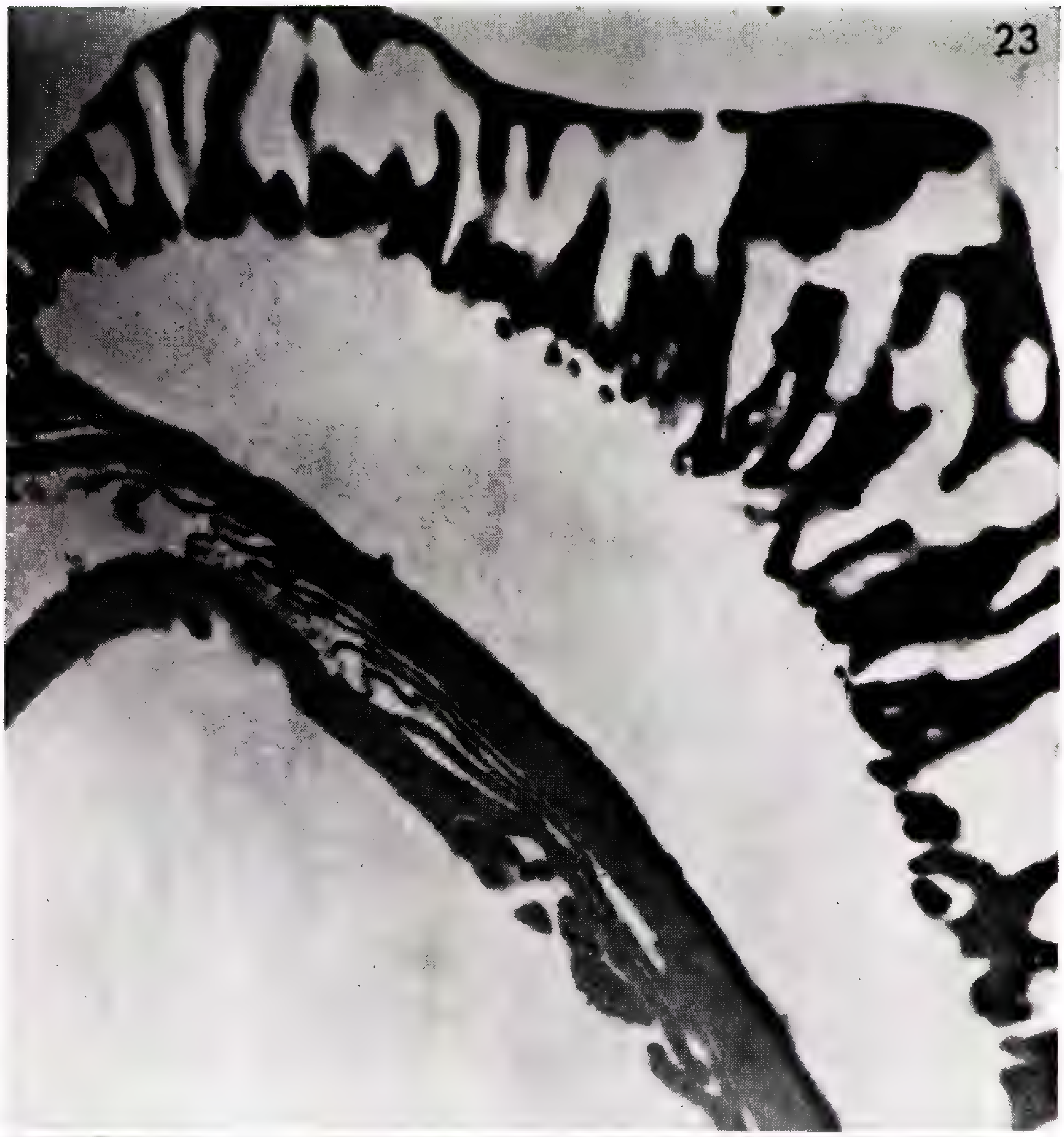


Fig. 21, 22. *Cacosmia rugosa* var. *arachnoides* (*Helenieae*). The endexine is thickened considerably in comparison to the foot layer. Near the interface with the foot layer, endexine lamellae can be recognized. The foot layer contains zones of lamellar microfibrils (arrows), but note that these lamellae do not penetrate the endexine. ca ×27,000. Fig. 22. Oblique section through colpus showing highly lamellate upper portion of the endexine. ca ×18,000 (Key to labeling, see Fig. 10).



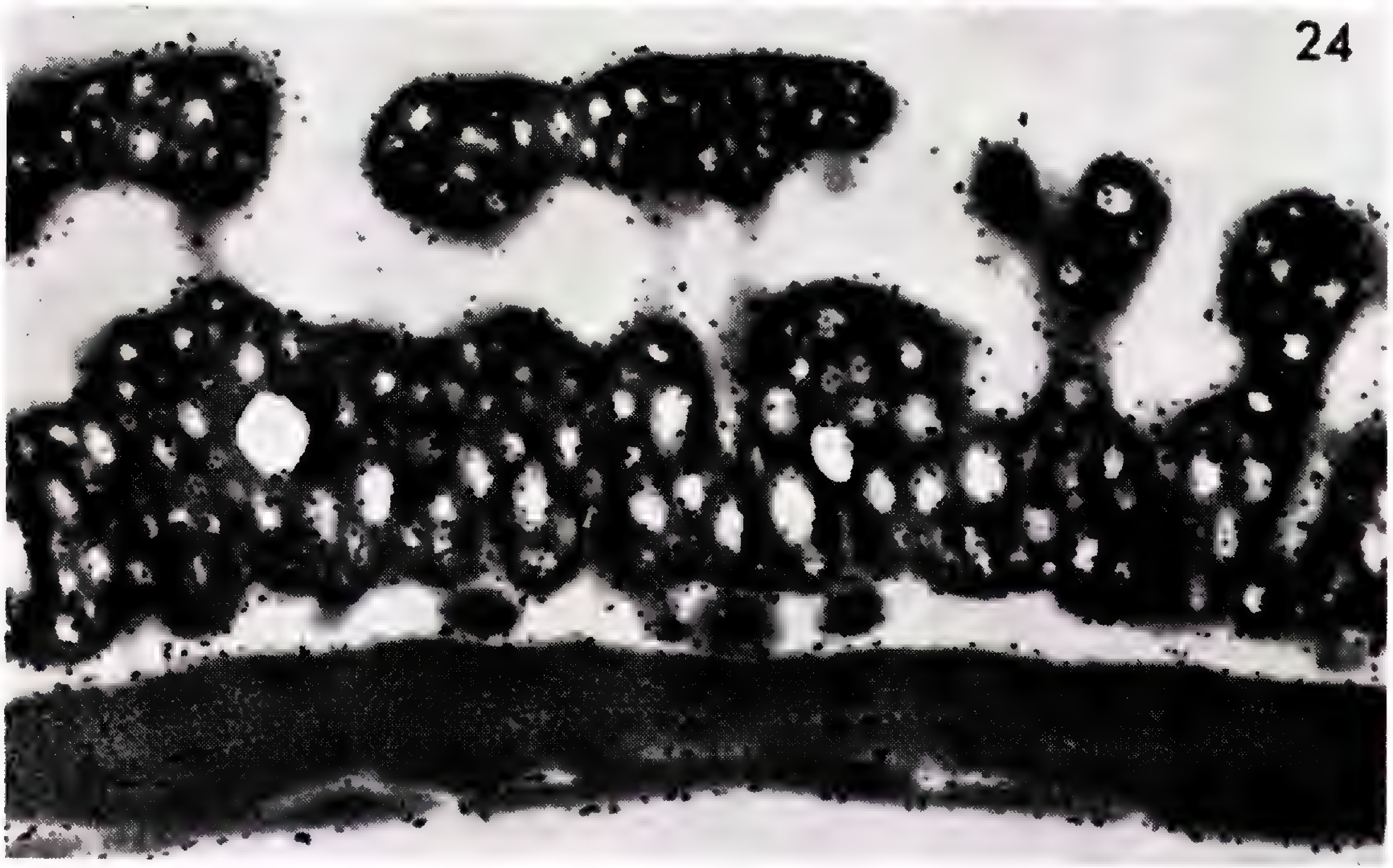


Fig. 23. *Amblyopappus pusillus* (*Helenieae*). Note lack of internal foramina and lamellate endexine. ca ×15,830. Fig. 24. *Hymenopappus newberryii* (*Helenieae*). Note thick columellar bases and numerous internal foramina. ca ×14,000 (Key to labeling, see Fig. 10).

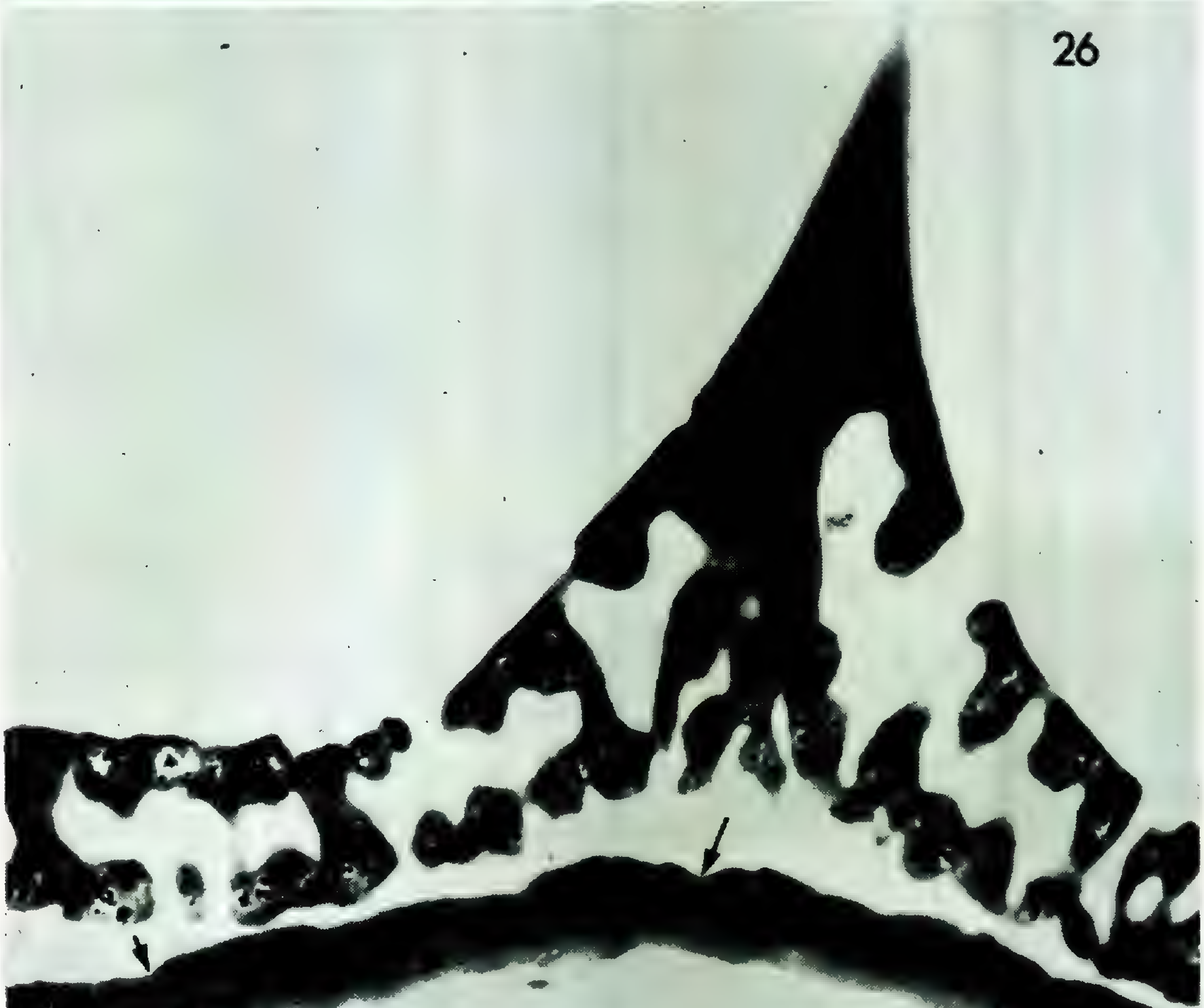
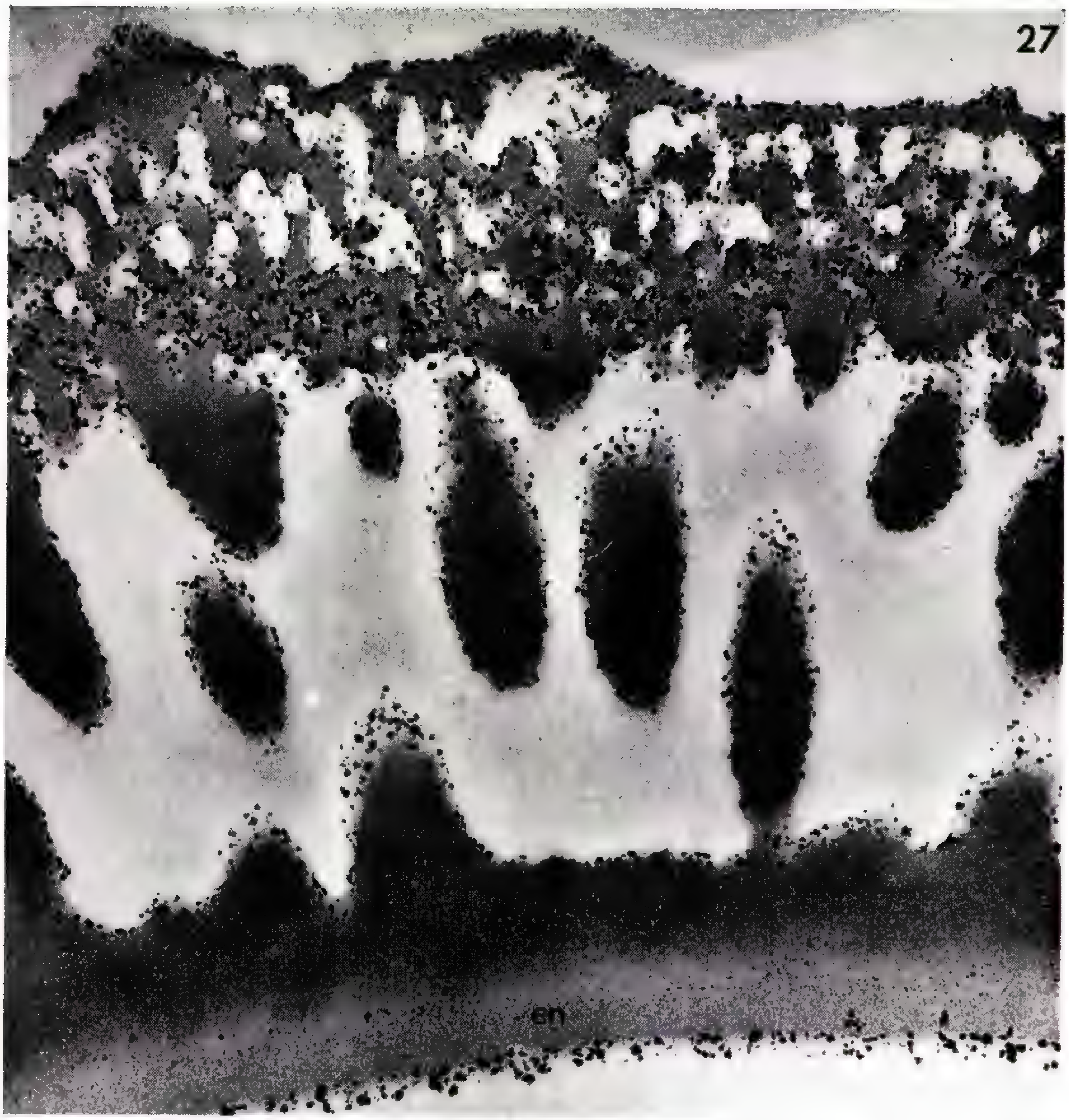


Fig. 25. *Lasthenia chrysostoma* (*Helenieae*). The internal foramina are filled with electron-dense material. ca ×7,500. Inset of *L. glabrata* emphasizes foot layer-endexine relationship. ca ×16,000. Fig. 26. *Palaxfoxia hookeriana* (*Helenieae*). The foot layer is very uneven along the upper surface (arrows). The endexine is almost totally lamellate. ca × 9,000 (Key to labeling, see Fig. 10).



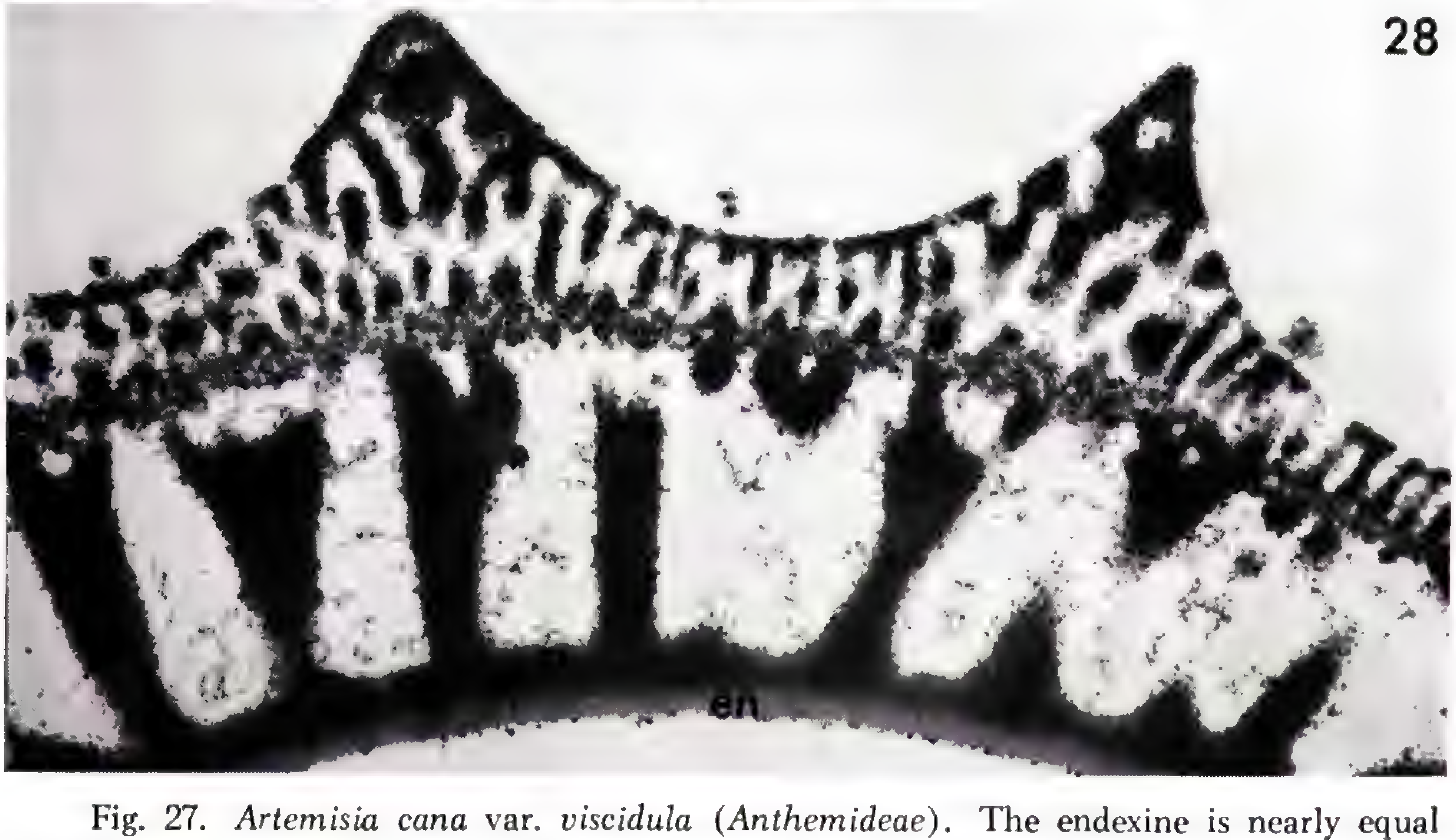
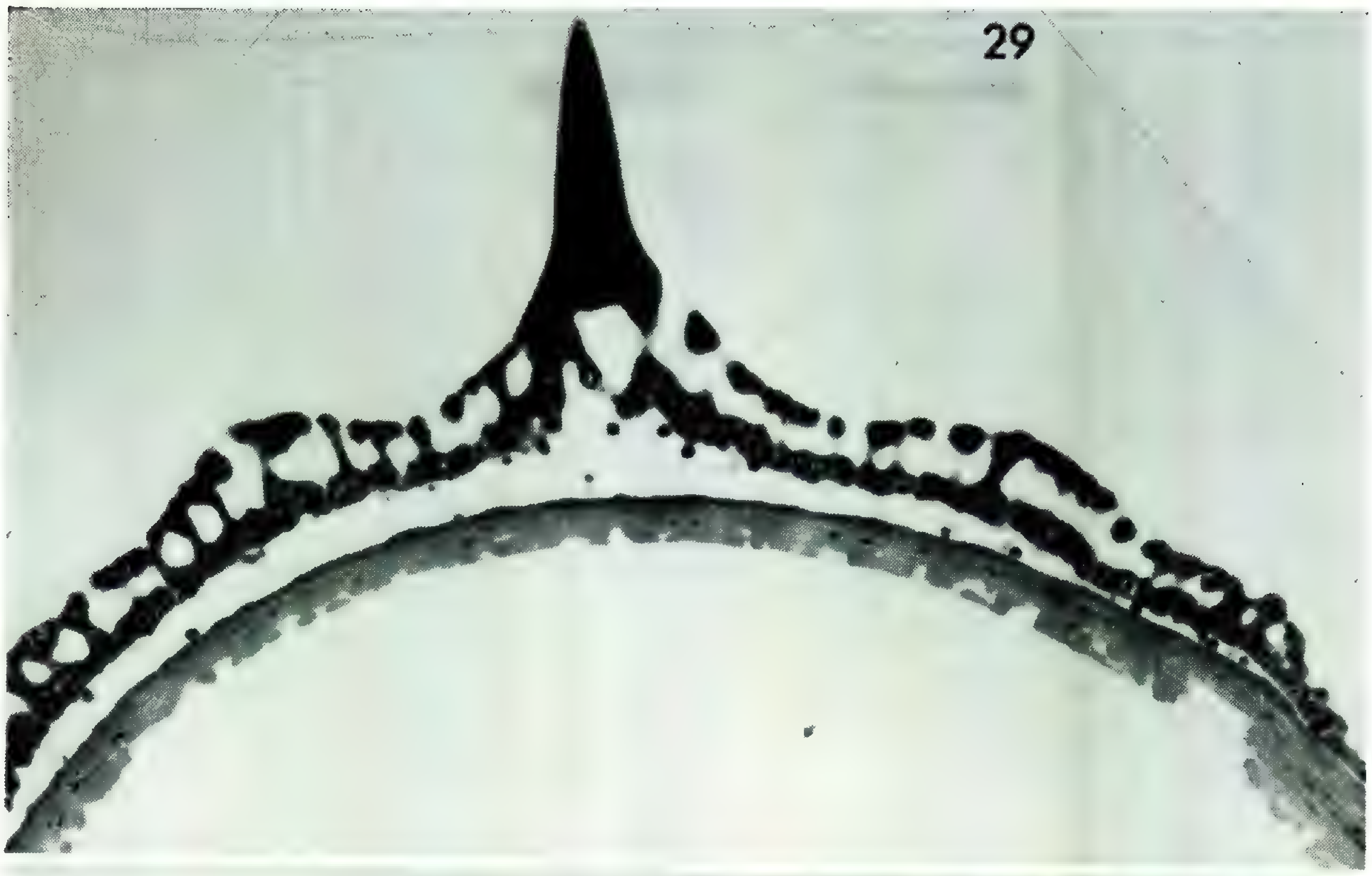


Fig. 27. *Artemisia cana* var. *viscidula* (*Anthemideae*). The endexine is nearly equal in thickness to the foot layer. Large columellae form numerous levels of internal tecta. (Plane of sectioning gives erroneous impression of columellae not being attached to foot layer.) ca ×40,500. Fig. 28. *Crossostephium turkestanicum* (*Anthemideae*). Internal tecta levels are fewer as compared to Fig. 27. ca ×11,200 (Key to labeling, see Fig. 10).



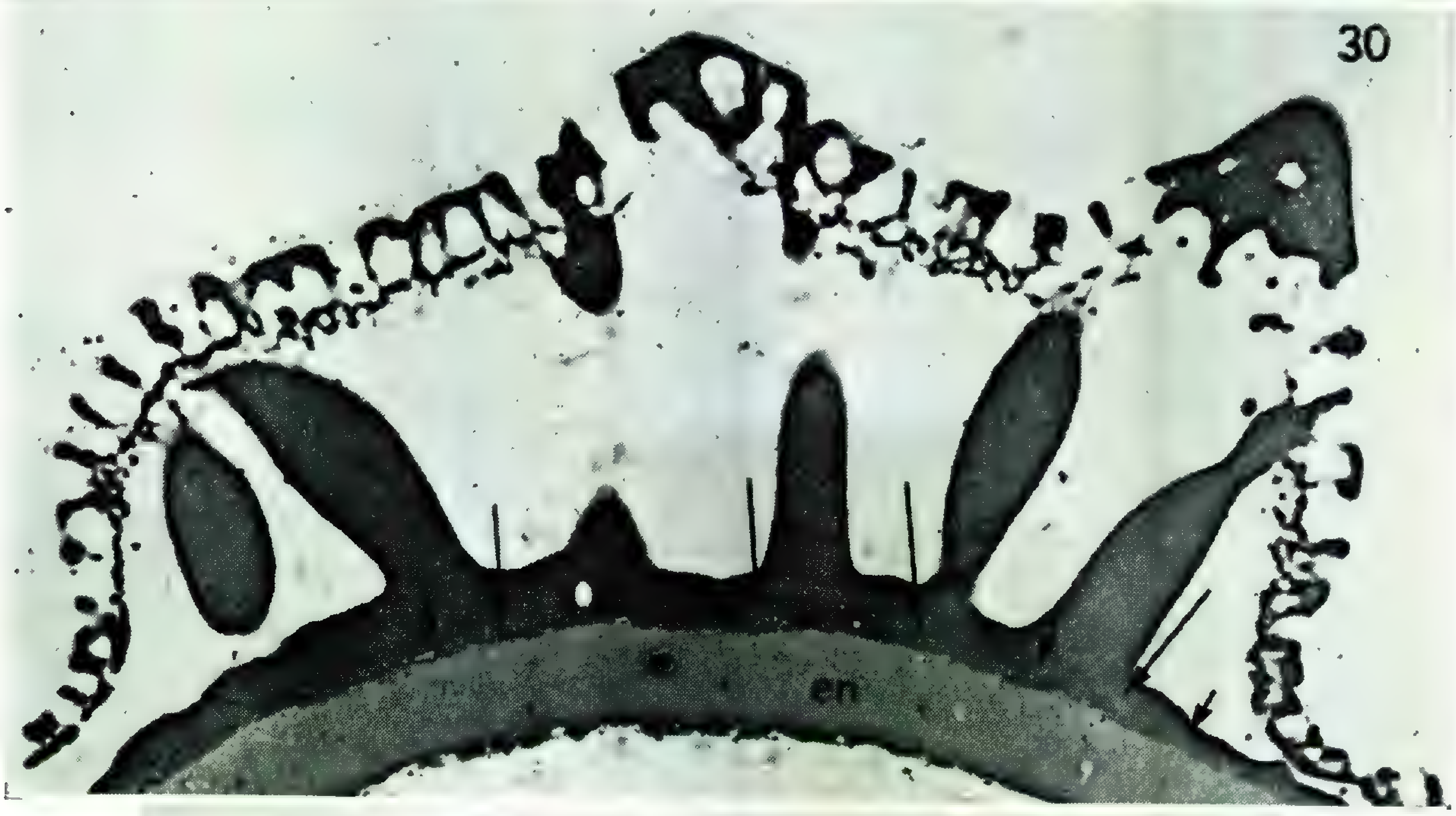


Fig. 29. *Schistocarpha platyphylla* (*Senecioneae*). Note similarity to Fig. 25 (*Helenieae*). ca ×6,500. Fig. 30. *Liabum caducifolium* (*Senecioneae*). Microfibrils (arrows) are barely perceptible in the foot layer. Note exine similarity to *Cacosmia* (Fig. 21). ca ×11,200. Fig. 31. *L. kluttii* (*Senecioneae*). Area comparable to arrows of Fig. 30. Arrows denote microfibril lamellae in foot layer. ca ×27,000 (Key to labeling, see Fig 10.)

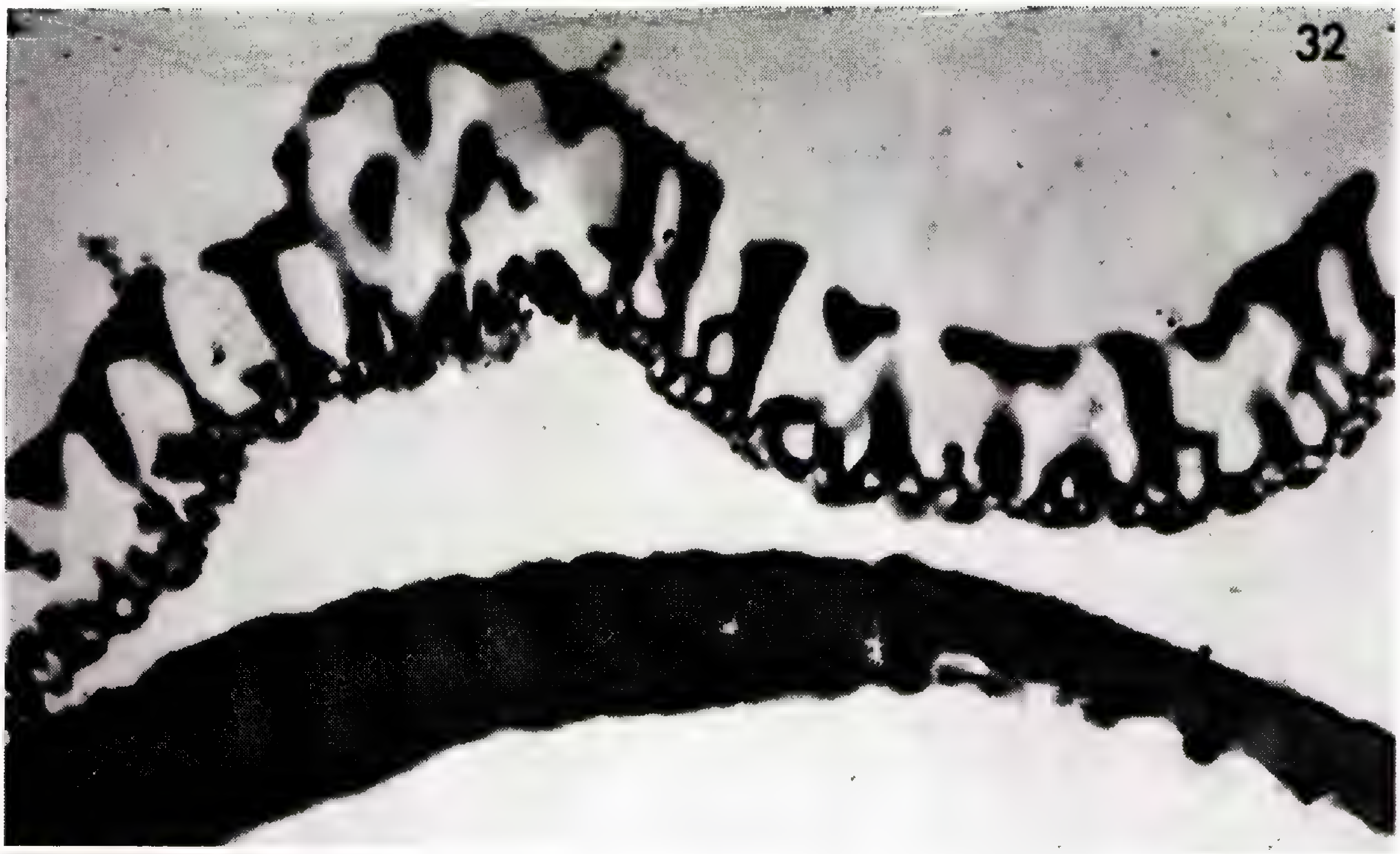


Fig. 32. *Didelta* sp. (*Arctotideae*). Columellar bases are markedly conjunct. A thin foot layer overlies an endexine of variable thickness. ca ×14,000. Fig. 33. *Berkheopsis diffusa* (*Arctotideae*). Low magnification electron micrograph illustrating complexity of exine. ca ×6,000 (Key to labeling, see Fig. 10).

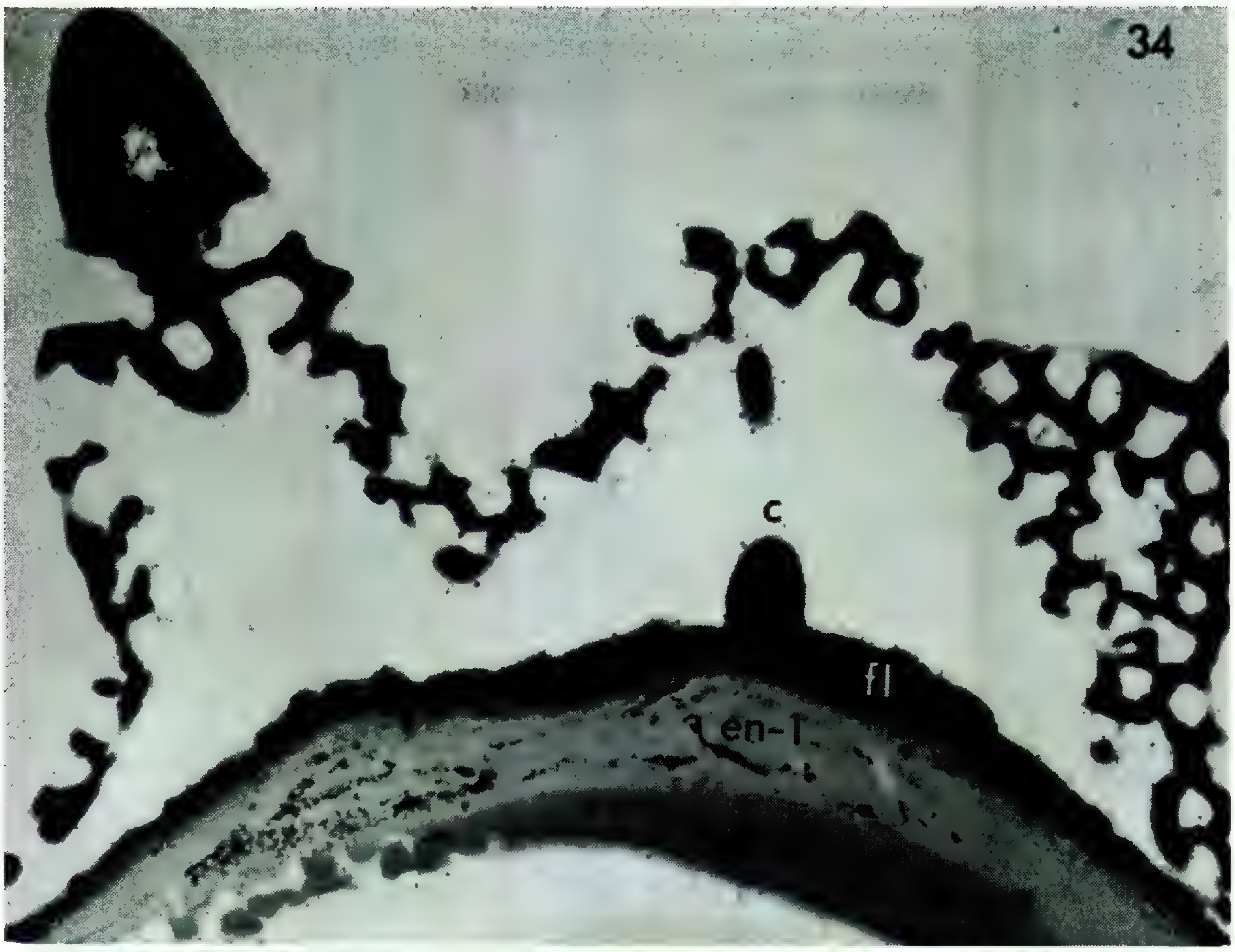


Fig. 34. *Moquinia volutina* (*Mutisieae*). The bilayered endexine is illustrated by (1) a dark gray layer (en-2) of variable thickness, and (2) a light gray layer (en-1) of consistent thickness. The columella (c) appears disconnected from foot layer as a result of plane of sectioning. Note large channel in spinule. ca ×16,000. Fig. 35. *Mutisia campanulata* (*Mutisieae*). Near median-equatorial view. Note complex ektexine above thick, digitate columellae. ca ×3,400. Inset represents area of Fig. 35 in brackets. Note thick lamellar tubules, with each containing a membrane core (represented by thin dark lines). Arrows indicate smooth gradation of lamellae into foot layer as well as the lower layer. ca ×12,500 (Key to labeling, see Fig. 10).

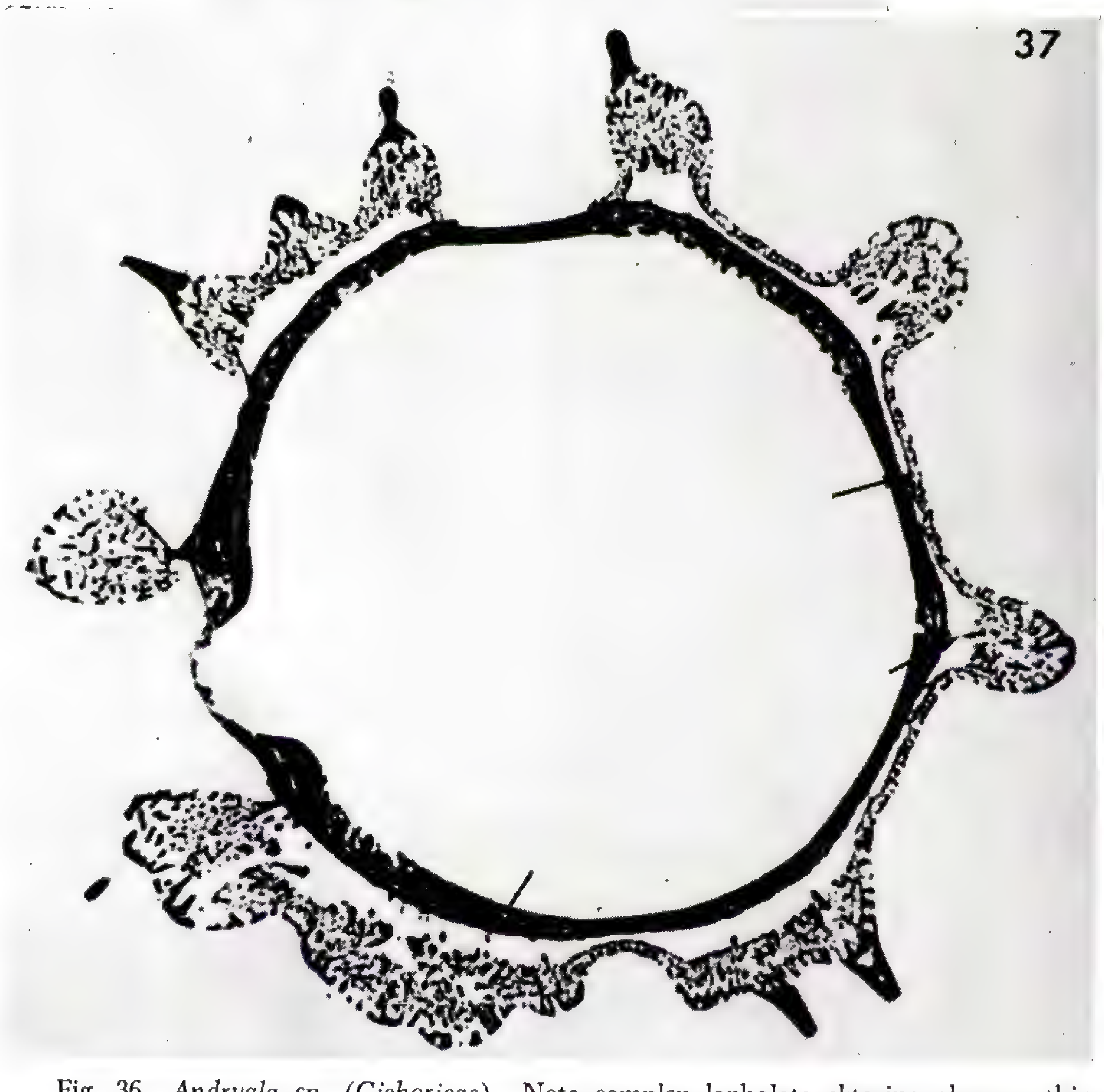


Fig. 36. *Andryala* sp. (*Cichorieae*). Note complex lopholate ektexine above a thin foot layer. ca ×9,000. Fig. 37. *Sonchus* sp. (*Cichorieae*). Low magnification electron micrograph illustrating generalized exine morphology. Note that lopholate and lacunar areas of exine show occasional attachment with the foot layer (arrows). ca ×5,000 (Key to labeling, see Fig. 10).

NOTES

CHROMOSOME NUMBERS OF OLDENLANDIA CORYMBOSA (RUBIACEAE) FROM SOUTHEASTERN ASIA[1]

Although few tropical species have been studied cytogeographically over a wide distribution, the weedy rubiaceous annual *Oldenlandia corymbosa* L. is an exception. The species occurs from southern United States to central South America, Africa, southern Asia including the Malayan Archipelago to New Britain and Queensland. Lewis (Grana Palynol. **5:** 300-341, 1964) summarized the known chromosome numbers of plants from four continents in which three cytotypes (2*x*, 4*x*, 6*x*) based on $x = 9$ were found. The diploid race was reported in the New World, the tetraploid in India and all three races in Africa, viz. the 2*x* common in western Africa, the 4*x* widespread in eastern and central Africa and rare in the western region and the 6*x* race from one locality in coastal western Africa. Recently the presence of the diploid race in Brazil was confirmed (Lewis, Ann. Missouri Bot. Gard. **53:** 102, 1966) as well as the hexaploid race in coastal Sierra Leone (Harvey, Taxon **15:** 162, 1966).

Even though the area studied in 1964 was extensive, it did not nearly include the whole range of *O. corymbosa* and in particular a large gap in chromosomal data existed for southeastern Asia and adjacent areas. However, I found that diploidy vs. polyploidy was directly related to size, exine thickness and aperture number of the pollen and that from herbarium material alone the ploidy level of plants could be judged. On this basis additional regions were assessed for presumed chromosome numbers to the limit of available herbarium specimens. In southeastern Asia, for example, a large disjunct diploid race was postulated even though supporting data from actual chromosome counts were lacking; elsewhere, the pollen data extended somewhat the known limits of races already established on chromosome numbers.

Early in 1966 I received a generous collection of seeds from Mr. S. R. J. White then traveling through Indonesia to Singapore. This material from five localities has now flowered at the Missouri Botanical Garden and verifies the existence of the diploid race in that area.

Oldenlandia corymbosa L.: **n = 9.** INDONESIA. JAVA: Bandung, *Lewis 6702* (MO), 1 plant, 42 km N of Jogjakarta, Lewis 6699 (MO), 1 plant; TIMOR: Atambua, Lewis 6703 (MO), 2 plants. SINGAPORE. *Lewis 6695* (MO), 1 plant, *Lewis 6696* (MO), 2 plants. All voucher specimens are from greenhouse grown plants.

Not only do the counts for *O. corymbosa* emphasize the usefulness and reliability of pollen data in distinguishing diploids and polyploids and extending, positively the known range of the 2*x* cytotype from Brazil and Texas through Africa to eastern Indonesia, but they further illustrate an example in the tropics of incipient speciation which can be initiated and enhanced by macrochromosomal muta-

[1] Supported by Public Health Grant No. 1 P10 ES 00139-01 ERT, from the Center for the Biology of Natural Systems, Washington University.

tions (to 4*x* and 6*x*), a phenomenon which I call cytocatalytic evolution (Lewis, in press).—*Walter H. Lewis, Department of Botany, Washington University and Missouri Botanical Garden, St. Louis.*

CLAYTONIA CAROLINIANA VAR. SPATULIFOLIA (SALISBURY) LEWIS, STAT. NOV. (PORTULACACEAE)

Claytonia caroliniana Michx. (Fl. Bor.-Amer. **1:** 160, 1803) var. **spatulifolia** (Salisb.) W. H. Lewis, stat. nov., based on *C. spatulaefolia* Salisb., Parad. Lond. *pl. 71*, 1807.

a. Blades of paired cauline leaves ovate (S.A. Fig. 3-4) to elliptic (S.A. Fig. 38-39); widespread at lower elevations in mountains of eastern North America to Minnesota .... var. *caroliniana*

aa. Blades of paired cauline leaves narrowly elliptic (S.A. Fig. 1-2) to narrowly ovate (S.A. Fig. 35-37) and obovate (S.A. Fig. 45-46); highest elevations of the Appalachians .... var. *spatulifolia*

Michaux described *C. caroliniana* with short-oval (cauline) leaves scarcely ½″ long from material probably collected in eastern Tennessee, ESE of Johnsborough on route to Iron Mountain (cf. Thwaites, André Michaux's travels in Kentucky, 1793-96, *In Early Western Travels 1748-1846*, **3:** 98, 1904). The description of cauline leaves matches the specimen housed in the Michaux Herbarium (P) recently sketched for me by M. Gérard G. Aymonin and reproduced here (Fig. 1). This represents the widespread broad-leafed variety which varies from ovate to elliptic (Fig. 2). The second variety is characteristically found at higher elevations in eastern North America, particularly common above 1,000 m in the southern Appalachian Mountains; it is well illustrated by W. Hooker in plate 71 of the *Paradisus Londinensis* (Fig. 3) though the specific name chosen by Salisbury describes the subspatulate basal leaves. Figures 4-5 show other common leaf shapes of the var. *spatulifolia* which resemble those of *C. virginica* L. except that they are much shorter. Where this species and the var. *spatulifolia* coexist in Tennessee, North Carolina and West Virginia, I observed no intermediate plants and the two taxa invariably differed in chromosome number. At lower elevations the var. *caro-*

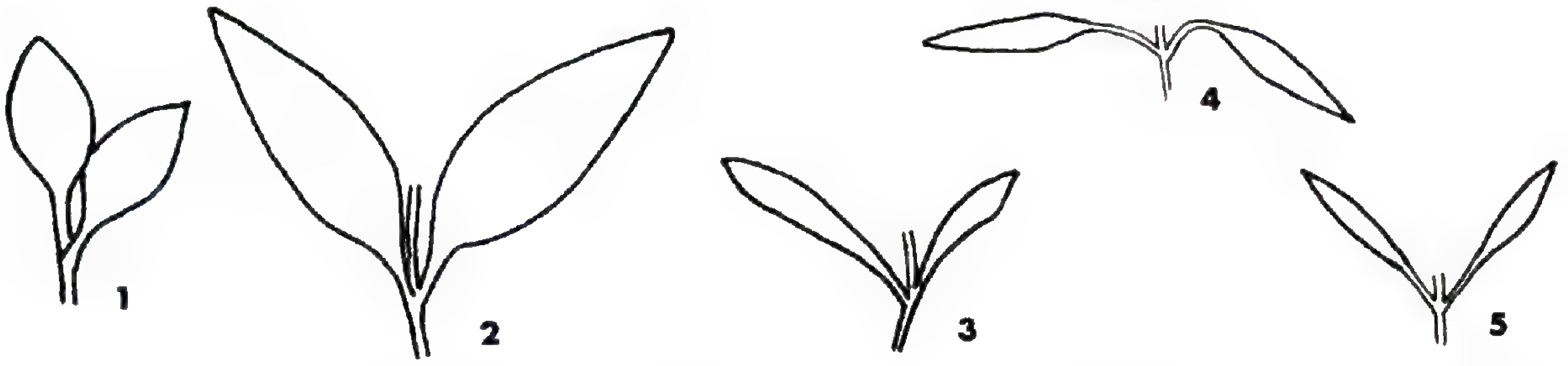


Fig. 1-5. Outline sketches (×1/2) of the single pair of cauline leaves of *C. caroliniana*. Fig. 1-2. Var. *caroliniana*. Fig. 1. *Michaux s.n.* (P). Fig. 2. *Soper & Fleischmann 6309*, Simcoe Co, Ontario (MO). Fig. 3-5. Var. *spatulifolia*. Fig. 3. *C. spatulifolia* by W. Hooker from Parad. Lond. *pl. 71*. Fig. 4. *Lewis 6675* (MO). Fig. 5. *Lewis 6660* (MO).

liniana and *C. virginica* also coexist, but again no intermediate was found from localities in these states.

Representative specimens of *C. caroliniana* var. *spatulifolia* (all MO): *Lewis 6652, 6653, 6654, 6657* (Sevier Co, Tennessee); *6659, 6660* (Swain Co, North Carolina); *6664, 6665, 6666, 6667* (Haywood Co, North Carolina); *6668* (Madison Co, North Carolina); *6675, 6677* (Preston Co, West Virginia).—*Walter H. Lewis, Missouri Botanical Garden, St. Louis.*

ADDENDUM: SCHLECHTER'S NEW GUINEA DUPLICATES OF LIPARIS (ORCHIDACEAE) AT THE MISSOURI BOTANICAL GARDEN

In an imaginative piece of detective work Woods (Notes Royal Bot. Gard. Edinburgh **26:** 361-364, 1966) describes the results of his search for Dr. R. Schlechter's orchid duplicates, the originals of which were destroyed by fire following the allied air raid on Berlin during 1-2 March 1943. The genus *Liparis* L. C. Rich. was selected as a test case.

Twenty-eight herbaria (including Edinburgh) were sent data sheets listing the 54 New Guinea species largely described by Schlechter from his own collections [in Fedde, Repert. sp. nov. regni veg. Beih. **1:** 181-220 (*Liparis*), 1911]. Recipients were requested by Woods to check the lists with their herbarium material and to amend and return the circulars. Response was apparently unanimous.

Five American herbaria were solicited, viz. Orchid Herbarium of Oakes Ames at Harvard's Botanical Museum (AMES), Field Museum, Chicago (F), New York Botanical Garden (NY), University of California at Berkeley (UC) and the U. S. National Museum (US). The results revealed that not a single sheet of New Guinea specimens of *Liparis* collected by Schlechter existed in the general collections of the American herbaria surveyed. Only the Ames Orchid Herbarium yielded results, and then just second to Leiden in total number of collections. The Missouri Botanical Garden Herbarium was not canvassed. Our general exchange with Berlin prior to World War II, however, was perhaps greater than any other American herbarium and with good reason, for the long-time Curator (1913-1948), Dr. Jesse M. Greenman, studied under Professor A. Engler at Berlin and received his Ph.D. there in 1901. Apparently this personal contact was a major factor in developing or at least maintaining a flow of specimens from Germany to St. Louis. This is well illustrated by the MO holdings of *Liparis* collected by Schlechter in New Guinea: a total of 18 specimens or more than F, NY, UC, US and the large European herbaria at Copenhagen, Munich, Uppsala, Utrecht, Vienna and Zurich, all which have none, and far more numerous than the totals at Paris and Brussels.

The species and specimens at MO, with Schlechter's numbers, are listed below.

Liparis altigena Schltr., *18706* (type), MO 923909.
L. anemophila Schltr., *17100,* MO 923920.
L. calcaria Schltr., *18027* (type), MO 923911.

L. caricifolia Schltr., *18590* (type), MO 923896.
L. chlorantha Schltr., *17147* (type), MO 923912.
L. confusa J. J. Smith (*L. flaccida* Schltr.), *16361*, MO 926742.
L. dolichobulbon Schltr., *17224*, MO 923922; *19054*, MO 923913.
L. graciliscapa Schltr., *19189*, MO 923926.
L. leptopus Schltr., *19629* (type), MO 926750.
L. mapaniifolia Schltr., *19322* (type), MO 926752.
L. melanoglossa Schltr., *17425*, MO 923893; *19526*, MO 923895.
L. nebuligena Schltr., *16961*, MO 923921.
L. neoguineensis Schltr., *16803*, MO 923915.
L. ovalis Schltr., *18056* (type), MO 923924.
L. persimilis Schltr., *18999* (type), MO 923908.
L. truncicola Schltr., *16674* (type), MO 923919.

Woods notes that the distribution of Schlechter's duplicates in other genera might follow a pattern similar to that found for *Liparis*. After selecting at random the small genus *Plocoglottis* Blume with 10 recognized species from New Guinea (Schlechter, loc. cit. 401-411, 1912), I suspect that Woods is correct. MO has three sheets of which two are type collections:

P. maculata Schltr., *19316* (type), MO 926713.
P. papuana Schltr., *17006*, MO 924072.
P. sakiensis Schltr., *18285* (type), MO 924071.

In tracing extant duplicates of Schlechter and others from Berlin, taxonomists should consider the likelihood of material at the Missouri Botanical Garden not only in the *Orchidaceae*, but in other families as well.—*Walter H. Lewis, Missouri Botanical Garden, St. Louis.*

MESECHITES PILOSISSIMA WOODSON (APOCYNACEAE) NEW TO PERU

Mesechites **pilosissima** Woodson, sp. nov.

Frutices volubiles per omnes partes plus minusve dense fulvo-pilosi superficie superiore foliorum excepta, caulibus gracilibus internodis elongatis. *Folia* longiuscule petiolata lamina late ovato-elliptica acute subcaudato-acuminata basi rotundata 10-17 cm longa 4-9 cm lata firmiter membranacea opaca subtus pallidore nervo medio basi supra pauciglanduligero, petiolo 1.5-2.0 cm longo habitu cirrhi saepe contorto. *Inflorescentia* alternatim axillaris dichotome bostrycinis densius pilosa penduculo petiolo subaequilongo pluriflora. *Flos* albidus pedicellis ca 1 cm longis, laciniis calycis latiuscle trigonalibus acutis ca 5 mm longis corollae salverformis tubo cylindrico ca 2.5 cm longo prope medium constricto ibique staminigero deinde paulo ampliato apicem versus ostio ca 3 mm diam lobis oblique dolabriformibus ca 1.2 cm longis patulis, antheris anguste oblongis ca 5 mm longis glabris, ovariis oblongoideis ca 2 mm longis minute puberulo-papillatis glandulis

nectarii depresse quadratis humilibus stylo gracili stigmate anguste umbraculiformi ca 4 mm longo. *Folliculi* juvenes graciles dense pilosi.

PERU. JAEN: forest, Cajamarca, alt 500 m, 27 March 1960, *Woytkowski 5604* (holotypus MO, isotypi G, GH, US).

Description of a new *Mesechites* is a rather distasteful task, but seems really necessary here. The flowers are so large and the pilose indument so copious that at first glance I mistook the specimen for an *Odontadenia.* Two other species of *Mesechites* are pubescent, but the indument is a rather inconspicuous puberulence and the flowers of each are about half the size of those of *M. pilosissima.—Robert E. Woodson, Jr., Missouri Botanical Garden, St. Louis* (posthumously).

PIPER AND PEPEROMIA (PIPERACEAE) NEW TO PANAMA

Piper **boquetense** Yuncker, sp. nov.

Frutex ca 1 m altus; internodiis floriferis gracilibus conferte villosis, pilis 0.5-0.75 mm longis. *Foliis* subrhombico-ellipticis, apice longe acuminatis, basi oblique valde inaequilateralibus, latere uno usque ad 5 mm breviore rotundatis obtusis latere longiore rotundatis cordulatis, a medio infero pinnatim venosis, venis utrinque 5-6, laminae facie supra glabra infra in venas pubescente; petiolo 2-4 + 3-5 mm longo conferte villoso sub base vaginato. *Bracteis* triangulari-subpeltatis fimbriatis. *Drupa* subglobosa glabra; stigmatibus sessilibus.

Shrub about 1 m high, branching; stem somewhat nodose, the upper internodes slender, 2-5 cm long, densely villous, the hairs 0.5-0.75 mm long, crisply erect. *Leaves* subrhombic-elliptical, long-acuminate at apex, the base obliquely inequilateral with one side up to 5 mm shorter at the petiole, rounded obtuse, the longer and wider side more rounded and cordulate, 6-8 cm wide and 14-17 cm long, glabrous above, the nerves beneath pubescent with the midrib subvillous, the hairs suberect, pinnately nerved to about the middle, the nerves 5 or 6 on each side, the uppermost continuing to the apex, with slender cross-connecting anastomosing nervules, drying chartaceous, translucent; petiole 2-4 + 3-5 mm long, or up to 1 cm on lower leaves densely villous, vaginate toward the base. *Spikes* 3 mm thick and 6-10 cm long, apiculate, the peduncle 10-12 mm long, pubescent, the bracts triangular-subpeltate with villous pedicel, the rachis ridges villous with the hairs nearly as long as the bracts, the stamens 3. *Fruit* subglobose, with convex apex and sessile linear stigmas.

PANAMA. CHIRIQUÍ: vic of Boquette, Finca Collins, alt 1650 m, 24 July 1959, *Stern, Chambers, Dwyer & Ebinger 1150* (holotypus MO, isotypus GH).

This species somewhat resembles *P. culebranum* C. DC., but differs in having more densely pubescent stems and more rhombic-shaped leaves which are broader below the middle and glabrous on the upper surface.

Piper **dukei** Yuncker, sp. nov.

Frutex ramosus nodosus, internodiis superis villosis retrorse hispidis, pilis usque ad 2 mm longis. *Foliis* subrhombico-lanceolato-ellipticis apice attenuatim longe-acuminatis basi inaequilateraliter rotundato-cordulatis supra villosis scabridis subtus villosis ad venas pro maxime, pilis erectis, valde ciliatis ad medium laminam pinnatim venosis, nerviis utrinque 6-7, petiolo brevi villoso ad basim vaginato. *Pedunculo* petiolum aequante, bracteis angustatis triangulari-subpeltatis subglabris. *Drupa* oblongo-cuneata apice truncata albida, stigmatibus parvis sessilibus.

Branching, nodose *shrub;* upper internodes slender, 5-6 cm long, moderately villous, the hairs suberect to reflexed, up to 2 mm long, intermixed with hispid understory of much shorter, retrorse hairs. *Leaves* subrhombic-lance-elliptic, with attenuately long-acuminate apex and inequilaterally rounded, cordulate base, one side 1-2 mm shorter at the petiole, the midrib up to 5 mm or more closer to the shorter side, villous above, the midrib densely so, harshly scabrid from the rigid hair bases, villous beneath with the nerves more densely so, the hairs erect, 1-1.5 mm long, strongly ciliate, 4-6.5 cm wide and 12-16 cm long, pinnately nerved to about the middle, the nerves 6 plus 7, with slender, cross-connecting, anastomosing nervules, finely glandular-dotted, drying brown, chartaceous, translucent; petiole scarcely 5 plus 1-2 mm long, villous, vaginate at the base. *Spikes* 2-3 mm thick and 6.5 cm long, apiculate; peduncle scarcely 5 mm long, villous; bracts pale, narrowly triangular-subpeltate, the lower angle narrowed and subcallose, glabrous above, or the dorsal angle with a few short bristles, the pedicel dorsally fimbriated; stamens 3 or 4. *Drupe* oblong-wedge-shaped, the apex truncate, whitened, the stigmas small, sessile.

PANAMA. PANAMA: Río Canita, along Pan-Am Hwy, open grazed area nr Jenine, 24 Sept 1961, *Duke* 3874 (holotypus MO, isotypus DUP).

The villous parts, attenuately long-acuminate apex of the strongly ciliate blades, and narrowly triangular floral bracts are distinctive feature of this species. It resembles *P. erubescentispicum* Trel. in some respects, but differs in its more strongly villous parts, more leaf nerves, and narrower and longer apex of the blade.

Piper **payanum** Yuncker, sp. nov.

Frutex parvus, internodiis floriferis gracilibus, crispo-villosis, pilis albis 1 mm vel ultra longis. *Foliis* elliptico-subovatis, apice acuminatis, basi oblique inaequilateralibus, latere uno ca 5 mm breviore subobtusis vel acutis, latere longiore rotundatis obtusis vel subacutis, deorsum pinnatim venosis, venis utrinque 6-7, laminae facie utrinque dissite villosa (ad venas quam maxime); petiolo 10-13 mm longo villoso fere ad medium vaginato. *Bracteis* triangulari-subpeltatis fimbriatis. *Drupa* glabra obpyramidali-trigona, stigmatibus sessilibus.

Small *shrub,* scarcely 1 m high; upper internodes slender, 2-5 cm or more long, crisp-villous, the hairs white, 1 mm or more long. *Leaves* elliptic-subovate, acuminate at apex, the base obliquely inequilateral with one side about 5 mm shorter at the petiole and subobtuse or acutish, the longer side more rounded and obtuse or

subacute, 7-9.5 cm wide and 16-22 cm long, rather thinly villous on both sides, the nerves more densely so toward the base, the hairs white, those along the nerves erect, slightly scabrous above, ciliate, pinnately nerved to about the middle, the nerves 6 or 7 on each side, with slender cross-connecting anastomosing nervules, drying chartaceous, translucent; petiole 10-13 mm long, villous, vaginate to the middle or above. *Spikes* 3 mm thick and 6 cm long, the peduncle about 1 cm long, thinly villous, the bracts triangular-subpeltate, coarsely fringed. *Fruit* glabrous, obpyramidal-trigonous, with truncate or somewhat depressed apex and small sessile stigmas.

PANAMA. DARIEN: trail Paya to Pucra, 11 June 1959, *Stern, Chambers, Dwyer & Ebinger 220* (holotypus MO).

The long-villous parts, leaf shape, type of bracts and shape of the fruit are distinctive characters of *P. payanum*. It differs from the allied *P. pseudogaragaranum* Trel. by its larger, scarcely cordulate leaves, longer petioles, which are vaginate to the middle or above, and more numerous veins. From *P. subulatem* C. DC., which it also resembles to some extent, the species differs in its longer petioles and peduncles and the shape of the drupes.

Piper **sternii** Yuncker, sp. nov.

Arbuscula ca 2 mm alta; internodiis floriferis dissite pubescentibus glabrescentibus. *Foliis* late rhombico-ellipticis, apice abrupte acuminatis, basi oblique inaequilateraliter acutis, latere uno 2-3 mm breviore ad petiolum, supra medio pinnatim venosis, venis utrinque 4-5, laminae facie supra glabra glandulosa, infra ad venas crispo-pubescente; petiolo ca 4-5 + 2-3 mm longo sub base vaginato. *Bracteis* triangulari-subpeltatis fimbriatis. *Drupa* trigona glabra, apice depressa; stigmatibus sissilibus.

Small "*tree*," about 2 m tall; "stem flecked with white," upper internodes 2-4 cm long, thinly pubescent glabrescent. *Leaves* broadly rhombic-elliptical, rather abruptly acuminate at apex, obliquely inequilaterally acute at base with one side 2-3 mm shorter at the petiole, 7-10 cm wide and 15-18 cm long, glabrous and rather thinly glandular-dotted above, the main nerves beneath crisp-pubescent, pinnately nerved to above the middle, the nerves 4 or 5 on each side, the uppermost strongly curving to the apex, with slender anastomosing nervules, drying thin, translucent, densely finely pellucid-dotted; petiole about 2-3 mm to 4-5 mm long, glabrate, vaginate toward the base. *Spikes* 2 mm thick and up to 12-14 cm long, the peduncle 10-13 mm long, glabrate, the bracts triangular-subpeltate, fringed. *Fruit* trigonous, glabrous, with depressed apex and sessile stigmas.

PANAMA. DARIEN: trail betw Paya & Pucro. in wet forested area, 12 June 1950, *Stern, Chambers, Dwyer & Ebinger 420* (holotypus MO, isotypi GH, US); bank above Río Paca, *Stern et al. 597* (MO).

Peperomia **ebingeri** Yuncker, sp. nov.

Herba delicatula prostrata patens, caule pergracile hirtulo pilis rigidis erectis. *Foliis* alternis orbicularibus vel rotundato-subovatis 3-4 mm latis utrinque glabris

margine valde setose-ciliato palmatim 3-nervis, petiolo dissite hirtulo; spicis terminalibus dissite florigeris, pedunculo hirtulo, rhachide verruculosa, bracteis rotundato-peltatis glabris vel saepe 1-3 setosis. *Drupa* globoso-ovoidea apice obliqua, stigmate subapicali.

Delicate, prostrate, spreading *herb*; stem very slender, hirtellous, the hairs straight, erect. *Leaves* alternate, orbicular or round-subovate, fleshy, 3-4 mm wide, glabrous on both sides, the margin prominently setose-ciliate, palmately 3-nerved with the midrib faintly branched upward, somewhat glandular dotted, with a lighter colored zone above along the nerves, drying translucent; petiole about 0.5 mm long, sparsely hirtellous glabrescent. *Spikes* terminal, loosely flowered, about 1 mm thick and 1-1.5 cm long; peduncle less than 1 cm long, hirtellous; bracts round-peltate, glabrous or often with 1-3 prominent seta-like hairs; rachis verruculose. *Drupe* globose-ovid, the apex oblique with subapical stigma, eventually exserted on a pseudopedicel.

PANAMA. CANAL ZONE: Barro Colorado, David Fairchild Trail, epiphytic on tree trunk, 24 June 1960, *Ebinger 165* (holotypus MO).

The slender stems, very small, round leaves, short spikes, and setose bracts are distinctive characters of this species. It differs from *P. rotundifolia* (L.) H. B. K. in its smaller leaves, type of indument, shorter spikes, and setose bracts. From *P. delicatula* Hensch. and *P. emarginella* (Sw.) C. DC., other similar small-leaved species, it differs by the type of fruit and the setose bracts.

Peperomia philipsonii Yuncker var. **panamensis** Yuncker, var. nov.

Foliis apice acutis supra dissite adpresse puberulis 9-plinerviis, nerviis vix subramosis.

This differs from the var. *philipsonii* from Colombia in the leaves being thinly pubescent above and more shortly pointed, and with nerves scarcely branched upward and confluent within the lowermost 1 cm.

PANAMA. PANAMA: Río Pita, 1-3 mi above confluence with Río Maestra, logging roads along Río Pita, 14 Oct 1961, *Duke 4756* (holotypus Mo, isotypus DPU).

—*T. G. Yuncker, DePauw University, Greencastle, Indiana* (posthumously).

PHOTOGRAPHS OF AFRICAN TYPE COLLECTIONS

Shortly after the second World War, the Missouri Botanical Garden Herbarium photographed about 4,000 type collections housed at the British Museum and the Royal Botanic Gardens, Kew. These are largely from tropical Africa with a few from the neotropics. Large (8 × 10 in.) prints are now available to other institutions on an exchange or purchase basis, hopefully at the rate of about 500 per year. Any institution wishing to receive a complete set or of particular taxa should write to Dr. Walter H. Lewis, Director of the Herbarium, Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis, Missouri 63110, U. S. A.

CONTENTS

Revision of the North and Central American hexandrous species of *Aristolochia (Aristolochiaceae)*,
by HOWARD W. PFEIFER 115-196

The genus *Erythronium (Liliaceae)* in Kansas,
by KENNETH R. ROBERTSON 197-204

Taxonomic status of *Claytonia rosea* and *C. lanceolata (Portulacaceae)*,
by DIANNE K. HALLECK and DELBERT WIENS 205-212

Pollen morphology and classification of the *Pyrolaceae* and *Monotropaceae*,
by JOAN W. NOWICKE 213-219

Systematic implications from electron microscopic studies of *Compositae* pollen—a review,
by JOHN J. SKVARLA and B. L. TURNER 220-256

NOTES 257-264

Chromosome numbers of *Oldenlandia corymbosa (Rubiaceae)* from southeastern Asia 257-258. *Claytonia caroliniana* var. *spatulifolia* (Salisbury) Lewis, stat. nov. *(Portulacaceae)* 258-259. Addendum: Schlechter's New Guinea duplicates of *Liparis (Orchidaceae)* at the Missouri Botanical Garden 259-260. *Mesechites pilosissima* Woodson *(Apocynaceae)* new to Peru 260-261. *Piper* and *Peperomia (Piperaceae)* new to Panama 261-264. Photographs of African type collections 264.

Volume 53 1966 No. 3

Annals
of the
Missouri Botanical Garden

The previous issue of the ANNALS OF THE MISSOURI BOTANICAL GARDEN, Vol. 53, No. 2, pp. 115-264, was published on November 7, 1966.

PUBLISHED BY THE BOARD OF TRUSTEES OF THE MISSOURI BOTANICAL GARDEN
AND WASHINGTON UNIVERSITY PRESS
ST. LOUIS, MISSOURI 63110

Annals
of the
Missouri Botanical Garden

A journal containing scientific contributions from the Missouri Botanical Garden and the Department of Botany of Washington University in affiliation with the Missouri Botanical Garden.

EDITORIAL COMMITTEE

WALTER H. LEWIS, *Editor*
Missouri Botanical Garden & Washington University

DEREK BURCH, *Missouri Botanical Garden & Washington University*
JOHN D. DWYER, *Missouri Botanical Garden & St. Louis University*
ANDRÉ ROBYNS, *Missouri Botanical Garden & Washington University*
GEORGE B. VAN SCHAACK, *Missouri Botanical Garden*

Information

THE ANNALS OF THE MISSOURI BOTANICAL GARDEN appears three times during the calendar year. Three numbers totaling about 400 pages constitute a volume.

Beginning with Volume 53, 1966:

Subscription Price	$15.00 per volume
Single Numbers	5.50 each

Contents of previous issues of the ANNALS OF THE MISSOURI BOTANICAL GARDEN are listed in the Agricultural Index, published by the H. W. Wilson Company.

Beginning June 1, 1962 the Stechert-Hafner Service Agency, Inc., 31 East 10th St., New York 3, N. Y., became sole agent for the ANNALS OF THE MISSOURI BOTANICAL GARDEN. The Agency handles all subscriptions, all claims beginning with volume 50 (1963) and all requests for back issues. Out-of-print number will be reprinted as may be required.

Under the arrangement with the Stechert-Hafner Service Agency, the Agency handles also all purchases of any portion of the ANNALS subseries known as the "Flora of Panama."

All matters regarding exchange continue to be handled by the Missouri Botanical Garden as in the past.

Printed by the Eden Publishing House, St. Louis, Missouri, 63103.

Annals
of the
Missouri Botanical Garden

Vol. 53 | 1966 | No. 3

CENTRAL AMERICAN AND WEST INDIAN SPECIES OF INGA (LEGUMINOSAE)[1]

BY JORGE LEÓN[2]
Missouri Botanical Garden, St. Louis

ABSTRACT

Four new species of *Inga*, *I. allenii*, *I. mortoniana*, *I. squamigera* and *I. tenuipedunculata*, are described among 56 recognized from Central America and the West Indies. The species are divided into three sections with the largest sect. *Inga* further segregated into 13 series many of which are reported as new.

Among the tropical American *Leguminosae*, the genus *Inga* Scop. is outstanding in the number and complexity of its species. Although Central America is at the northern extreme of their geographic distribution, the many endemics and the intense cultivation of some species make this area particularly interesting for a monographic study. An attempt of this kind was made by Pittier (Jour. Dept. Agr. Porto Rico **13:** 117-177, 1929) who had years before composed a general revision of the genus (Contr. U. S. Nat. Herb. **18:** 173-224, 1916). Pittier dealt with the Central American species as a unit independent of the South American group; this fact and his inadequate herbarium representation, as well as the unnecessary creation of new series, restrict the general usefulness of his monographs. The only other treatment for the whole area was by Britton & Rose (N. Amer. Fl. **23:** 2-16, 1928) which, as pointed out elsewhere (Schery, Ann. Missouri Bot. Gard. **37:** 189, 1950), is of limited use. Britton & Killip (Ann. N. Y. Acad. Sci. **35:** 110-124, 1936) studied the *Mimosaceae* of Colombia and their work is important in relation to the Panamanian species.

---

[1] Submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Washington University in affiliation with the Missouri Botanical Garden.

[2] Present address: Instituto Interamericano de Ciencias Agricolas de la OEA, Lima, Peru.

ANN. MISSOURI BOT. GARD. **53** (3): 265-359, 1966.

The previous issue of the ANNALS OF THE MISSOURI BOTANICAL GARDEN, Vol. **53**, No. 2, pp. 115-264, was published on November 7, 1966.

Differing from previous revisions, the one offered here considers the representation of *Inga* in Central America and the West Indies as a part of the South American complex. One result of this interpretation has been to reduce many names and to revive some old ones, notably several by Willdenow.

The standard herbarium techniques have been used in this study. However, field work in Central America plus mass collections of two cultivated species have helped considerably in the understanding of the range of variation.

History of the Genus

Plumier (Nov. Pl. Amer. Gen. 13, *t. 19,* 1703) was the first to describe *Inga* as a genus basing the name and characters on the description of Marcgravius (Hist. Pl. Bras. 111, 1648) and employing the vernacular name applied in Brazil to these trees. Linnaeus (Hort. Cliff. 209, 1737; Sp. Pl. 516, 1753) included it within *Mimosa* where it was maintained until Scopoli (Introd. 298, 1777) reinstated its generic rank. (For details of early history, see Gutiérrez, Rev. Fac. Nac. Agr. Colombia **7:** 27-33, 1947).

During the subsequent decades the concept of the genus was extended to cover many species that are now included in allied genera, such as *Pithecellobium, Calliandra, Zygia, Acacia,* etc. This was owing mainly to the splitting of *Mimosa* as understood by Linnaeus, as well as to the discovery of many systematic novelties. Such a wide sense for *Inga* was held by de Candolle (Prodr. **2:** 432, 1825), Martius (Flora **20:** 113, 1837), Kunth (Mimos. 35, 1819; Nov. Gen. Sp. Pl. **6:** 283, 1823), and especially by Willdenow (in L., Sp. Pl. **4:** 1004, 1806) to whom many modern authors attribute the authorship of the genus.

Our present interpretation is based on that of Bentham (in Hook., Lond. Jour. Bot. **4:** 577, 1845) who restricted *Inga* to the once-pinnate-leaved species of the American *Acaciae.* Later, in his classic monograph of the *Mimosae,* Bentham (Trans. Linn. Soc. **30:** 600, 1875) created the tribe *Ingae* to accommodate *Lysoloma, Calliandra, Enterolobium, Pithecellobium, Inga, Affonsea,* etc. Within the tribe, *Affonsea* and *Inga* are differentiated again from the other genera by their once-pinnate leaves. In more recent times this delimitation of Bentham has suffered only one important change: a group of Central American species with the above-mentioned characteristic has been separated from *Inga* on account of their very distinct fruits, and placed in *Pithecellobium* § CAULANTHON, a taxon to which Britton & Rose (N. Amer. Fl. **23:** 29, 1928) gave a generic rank under the name *Cojoba* (s.s.).

Affonsea St. Hil. is the genus most closely related to *Inga.* Bentham found it difficult to differentiate these genera on foliage characters alone; *Affonsea* seems to be an old or primitive genus with a several-carpelled gynoecium, a character that once in a while appears in *Inga,* probably a remainder of an ancient and common stock. The maintenance of *Affonsea* as a separate taxon based on an important floral character is confirmed by its geographic distribution that centers around the ancient geological shield of southeastern Brazil.

Morphology

Habit. All the species of *Inga* are well developed trees varying from 3 to 25 m tall in the Central American species. The tallest species, *I. altissima* Ducke of the Amazon, sometimes reaches more than 40 m while one of the smallest, *I. cookii* Pittier of Guatemala, stands only 3-4 m, an unimportant element in the cloud forest. *Inga* often exhibits the typical mimosaceous pattern of branching, forming an umbrella-like top; but more commonly its branching is profuse and irregular. Little is known of its root system; the experience of coffee growers tends to mark some species, especially those of § BOURGONIA, as trees with a highly divided and shallow system; in § INGA the branching is less frequent and deeper. Some of the rain forest species have poorly developed buttresses.

Indument. The indument found upon the young parts and flowers tends to disappear with age in the majority of the species, although in some it is permanent. It offers good key characters in the delimitation of sections and series, and even in the diagnosis of some species it may profitably be used. A dense, ferrugineous pubescence is characteristic of some species in ser. CALOCEPHALAE, while in ser. VULPINAE two main types are found, both ferrugineous; short and sparsely pilose or setose. The flowers in ser. DYSANTHAE are covered with a lanose indument. In § BOURGONIA, in contrast, the pubescence is scarce, and restricted to the nerves of the leaves and the tips of the perianth whorls. As usual in the family, the hairs are unbranched and glandular, and often have a typical thickening at the base.

Leaves. The leaves of *Inga* are once-pinnate, an unusual pattern in the *Mimosaceae.* The shortly petiolulate leaflets are arranged oppositely on a winged or cylindric rhachis, the terminal leaflet lacking and replaced by a linear appendix. The leaflets are slightly longer on one side of the rhachis, giving a somewhat asymmetric appearance to the whole leaf; in the uppermost pair they are larger and have narrow and oblique bases, while in the lower pairs they decrease in size and the base tends to be broader and symmetric. The leaflets are bifacial, more glabrous and lustrous above, with denser pubescence and prominent nerves beneath. According to the observations of Coester (Ueber die anat. Charak. der Mimos. 159-173, 1894) the internal structure of the leaves is very similar in the species that belong to the same series.

The rhachis has received considerable attention as a taxonomic character. It has been used to separate sections and series, based on its terete or winged appearance, and plays an important role in most keys at the specific level. Although in some instances it furnishes a rather constant character its usefulness probably has been overemphasized, for in the same species it may vary from broadly winged to subalate (wings in the upper section only) to completely terete (*I. oerstediana,* etc.)

A very striking feature is the presence of well developed interfoliolar glands. This type of extrafloral nectary is probably more complex in this genus than in any other of the *Leguminosae* and its function and development are practically unknown. Such glands correspond to the rhachial type (Zimmermann, Beih. Bot. Centralb. **49:** 175, 1932) and as a rule are solitary at the insertion of the folioles,

although in some species, as *I. hayesii*, they are commonly found in pairs. In *I. goldmanii* they also occur on the midrib of the leaflet near its insertion on the rhachis; similar cases are found only in *I. adenophylla* and *I. pruriens* of South America. The shape of these glands varies from filiform and curved, in *I. saffordiana*, to thin and conic in ser. VULPINAE, to short and patelliform in ser. INGA; finally, in some species the glands are practically obsolete. Their shape and size varies with the age of the plant, being better developed in the young leaves and seedlings and often non-existent in the old leaves. As a key character they have received too much attention; their main importance is as a secondary character in separating sections or series rather than at the variable specific level. The extra-floral nectaries in *Inga* attract many insects. In the Piarco swamp, in Trinidad, the author observed in *I. pilosula* that they are used as traps by large red ants to capture smaller insects.

The growth of new foliage may occur simultaneously with the opening of the flowers, as in *I. ruiziana*, immediately thereafter, as in *I. marginata*, or completely independently of flowering, as in *I. densiflora*. The young leaves appear in conspicuous terminal flushes and are often, as in many tropical plants, bronze to red in color and of very delicate texture. The color of the new foliage differs according to the species and varies from light green (*I. mortoniana*) to pink (*I. marginata*) to ferrugineous red (*I. edulis*), and only lasts for a few days. During these short periods the trees present quite an attractive aspect. Observations on *I. marginata* in two localities with very different climates, and for several years, show that new flushes occur almost every two months, and that their occurence does not seem to be related to external factors but to the internal rhythm of the plants.

Proliferations. In certain species, particularly in *I. punctata, I. sapindoides* and *I. edulis*, large proliferations occur on the branchlets. Their formation has been attributed, in the cultivated *I. feuillei* of Peru, to the action of bacteria. These spherical structures attain a diameter up to 4-5 dm, and are formed by a proliferous and condensed ramification covered with calyx-like structures which open in age to disclose many minute buds subtended by bracts; normal or reduced leaves seldom appear.

Inflorescence. The basic structure of the inflorescence in *Inga* is the raceme. The most common form is a simple raceme that appears solitary or in groups, either terminal on the new growth or axillary on the defoliated nodes of the older wood, subtended by free or whorled bracts. Some species offer particular variants: for example, in *I. mortoniana* the racemes are grouped on short spurs on the branches, leafless but with a terminal vegetative bud; in other species the flowers appear on a terminal shoot, also without leaves, which at the end of the flowering season continues its growth and produces new leaves (*I. ruiziana*, etc.). In *I. saffordiana* flowers have been reported to grow on the trunk and main branches, but it is more probable that they are produced on a thick spur rather than directly from the trunk. This is the only reported instance of cauliflory in *Inga*, although it is of common occurrence in the allied genus *Pithecellobium*.

The axis of the inflorescence is divided into a lower peduncular portion and a

floral rhachis. The peduncle varies from slender, sometimes filiform, to stout and woody. In some species of § BOURGONIA it is characteristically short, giving a cylindric appearance to the inflorescence; the floral rhachis is restricted in the other groups to the upper part of the axis. The flowers are subtended by bracts, which are persistent in some groups (ser. TETRAGONAE), caducous in others (ser. INGA).

The transition from raceme to spike is frequent in many species and in some is a permanent character. A further development in the structure of the inflorescence in *Inga* is attained when the raceme is contracted into a short, mace-like receptacle with the individual flowers arranged in compressed spirals, thus giving to the inflorescence a spherical appearance. In several species, as *I. heterophylla* and *I. quaternata*, it is possible to observe intermediate stages between a short raceme and a globose inflorescence even in the same branch. Bentham created two sections to accommodate all species with a mace-like receptacle: § LEPTINGA, where all the flowers are markedly pedicellate, and § DIADEMA, with flowers sessile or almost so. A study of the groups shows all kinds of intermediates and for this reason no validity is here assigned to § DIADEMA; Ducke (Bol. Tec. Inst. Agr. Norte **18:** 20-34, 1931) and Macbride (Field Mus. Publ. Bot. **13:** 6-47, 1943) have discarded it in local treatments of the genus.

Several flushes of flowers occur during the year and the blooming period may be different for species growing side by side. The inflorescences burst into bloom simultaneously over wide areas in a typical mimosaceous fashion (Burkart, Darwiniana **8:** 33, 1948), and last for only a few days. The flowering is acropetal, and many of the upper buds never develop. Anthesis is more frequent during the afternoon and the flowers are visited by many species of insects, particularly *Coleoptera*.

Flowers. The arrangement of the flowers in the inflorescence of *Inga* follows an irregular, often spiral pattern. The flowers vary from sessile to long-pedicellate in the same species; common in ser. INGA is a type of pseudopedicel developed at the expense of the lower part of the calyx.

According to Thompson (Publ. Hartley Bot. Lab. **7:** 47-50, 1931), the different parts of the flower are arranged on a spiral pattern following a 2/5 sequence. There is a more or less well developed receptacle on which are based the calyx, the corolla, the staminal tube and the gynoecium. The corolla and the staminal tube are fused for some distance at the base, a character that Baillon (Hist. Pl. **10:** 45, 1870) mentions also to occur in certain other groups of the *Mimosaceae.* A. Richard (Nouv. Élém. Bot. **2:** 221, 1833), assuming a receptacular nature for this fusion, was led to conclude that the calyx, whose insertion is inferior to this level, is not actually a calyx but an involucre. Observations of many flowers show that the calyx is inserted on the receptacle, although this is not completely clear in some cases owing to its thickening at the base. De Candolle (Mém. Leg. **1:** 39, 1825) considered the staminal tube and the corolla as hypogynous and mentions the occurrence of a similar receptacular structure in the *Swartzieae.* In some species there is an inconspicuous disc, between the staminal tube and the gynoecium, that possibly represents an inner reduced whorl of stamens.

The calyx consists of five valvate segments, united to form a tubular structure in the majority of the species, although campanulate in § BOURGONIA and in *I. saffordiana* broadly turbinate. The five divisions or teeth are generally of equal size, but in some species such as *I. acuminata,* they are very irregular, some becoming obsolete. The calyx, in shape and size, furnishes perhaps the best taxonomic character in the genus.

The corolla is always gamopetalous, tubular to tubular-funnelform, short or elongate; the relative size and shape, as well as the indument, are of importance in both specific and sectional delimitation. The total length of the corolla was used by Pittier (Jour. Dept. Agr. Porto Rico **13:** 122, 1929) to separate the § PSEUDINGA Benth. into two subsections: TENUIFLORAE, with the corolla less than 2.5 cm long, and GRANDIFLORAE, with the corolla more than 2.5 cm long or, if shorter, then very broad. The indument is sparsely to densely pilose and generally appressed, and is always found on the outside only.

The androecium consists of numerous stamens fused at the lower part of the filaments into a definite tube of irregular thickness. The tube is exserted or included in relation to the corolla and, although many authors have founded specific differences on this character, it is in general without any sound taxonomic significance. The number of stamens varies so widely in the same species that it also is of restricted use. The filaments at anthesis are the most conspicuous part of the flower; they are white in most of the species, but yellow in *I. pilosula,* while in ser. DYSANTHAE there is a pinkish tinge both in the corolla and the filaments. The two-celled, eglandular anthers contain in each theca two massulae formed by 16, 24, or 32 pollen grains which tend to remain together after shedding; this is probably one of the main factors determining the high sterility in *Inga.*

The gynoecium is formed by a sessile or slightly stipitate carpel ending in a filiform style usually longer than the staminal filaments. The ovary is elongate, with two series of anatropous ovules on the ventral placenta. The shape and indument vary in the different species. The style bears a discoid, entire or dissected stigma.

Fruit. The fruit in *Inga* varies from thin and dry to thick and fleshy. It has no definite pattern of dehiscence. Externally it shows four sides: two corresponding to the "margins" or vascular strands; the other two to the valves or intermediate areas. The different development of these four sides has produced three main types of legumes: 1) flat, when the valves are very broad in relation to the vascular margins—this is by far the most common type; 2) tetragonal, when the four sides have more or less the same width; 3) subterete, if the marginal faces are as wide as the valves or wider. In this case the development of vascular bundles gives a twisted, rope-like appearance to the legume. Intermediate types occur, but the general morphological characters mentioned above are of great significance in delimiting sections and species.

The fleshy structure of the legumes in *Inga* was the main character used by Willdenow in separating that genus from *Acacia, Mimosa,* etc. Although in some species the valves are thick and have a fleshy endocarp at maturity *(I. jinicuil, I. densiflora,* etc.), in the majority the walls of the fruit are thin and rather dry.

Seeds and germination. From the biological standpoint the seeds of *Inga* are the most interesting part of the plant, owing to the nakedness of the embryo and its "viviparous" germination. The first observations on this phenomenon were by Borzi (Rendic. Lincei **12:** 131-140, 1903) who, in a classic paper, dealt in considerable detail with the seeds of *I. feuillei* DC., introduced at the botanic garden in Palermo. Similar observations made on Central American species permit a broader picture of the phenomenon.

The young seed is completely covered by a thin, pulpy testa that in age develops a series of layers derived, according to Borzi, from the malpighian stratum. The outer layers are formed by white, brilliant, thin-walled cells, rich in sugar and of a cotton-like appearance, while towards the inner side of the seed-coat the cells tend to be thicker and less juicy. This white, fleshy aril, referred to in the old publications as the 'pulp,' is the main edible part of the legume, and through selection has attained considerable thickness in some varieties.

When the seeds reach maturity the seed-coat opens at the distal end along longitudinal sutures, owing to the growth of the cotyledons, and eventually becomes completely separated from them, leaving the embryo naked; the dark green cotyledons tightly enclose it, their bevelled and undulate margins being complanate except at one end where each divides into two lobes, the four lobes forming a cavity through which the radicle eventually emerges. At maturity the cotyledons start to separate but generally with not enough force to cause the dehiscence of the pods; the radicle, nevertheless, starts growing and may attain several centimeters in length before the eventual opening of the legume, if indeed this ever dehisces. The growth of the plumule is meanwhile kept at a very low rate.

When the legumes are mature the splitting of the valves is often helped by birds, especially *Psittacidae* which visit the fruiting trees in large flocks. They open the pods, remove the seeds, eating the aril and allowing the embryos to escape and fall to the ground. Other animals and even man contribute likewise to the dispersal. Once the embryo reaches the ground, the already advanced germination accelerates and the hypocotyl develops rapidly, growing in a spiral. As a protection against excessive transpiration and high temperatures it is covered with minute, ferrugineous hairs in some species, while in others the outer cells are filled with a red pigment. The cotyledons, which have a large supply of food, are protected from the loss of water by several layers of cutinized cells rich in tannin that permits them to be subjected to considerable desiccation without affecting the growth of the seedling. The embryos, however, lacking a protective coat, have to find a very favorable habitat in order to develop; this is partially compensated by the large number of seeds produced per tree despite the high floral sterility. The frequent occurence of larvae of *Diptera* (*Anestrepha* ssp.) also contributes to prevent possible overpopulation.

Geography

The geographic distribution of *Inga* is restricted to the American tropics with some penetration into temperate areas both north and south. The total range extends from Durango and Coahuila (25° N) to the delta of the Plata River (34° S).

The collections available indicate that most of the species have continuous ranges. Some of them are very wide: from Mexico to Brazil (*I. vera, I. punctata, I. quaternata*); from Guatemala to Brazil (*I. thibaudiana*); from Costa Rica to Paraguay (*I. marginata*). The center of speciation appears to be the Amazon basin where, according to Ducke, there are 89 species. From this area the number diminishes in all directions. We find towards the south: Matto Grosso, 9 spp; Rio Grande do Sul, 4 spp.; Uruguay, 2 spp.; towards the north: Venezuela, 30 spp.; Trinidad, 11 spp.; Guadeloupe, 3 spp.; Guatemala, 15 spp.; Coahuila, Mex., 1 sp. It is difficult at present to locate secondary centers of speciation, but recent explorations in western Colombia show that this area is second only to the Amazon basin in number and complexity of species.

A similar pattern of distribution is observed in the different sections and series which are richer in species in the Amazonian region and have an area progressively restricted in all directions.

Despite what some morphological characters would suggest (Stebbins, Amer. Nat. **86:** 40, 1952), it seems that all species in this genus tend to grow in mesophytic to hygrophytic habitats. The frequency rate in the Amazon, according to Ducke, shows that in the hyleia, *Inga* is the predominant *Leguminosae*, in the capoeiras and the mata virgem their number is still high, while they are lacking completely in the campinas or campos altos. A similar distribution is found among the dry and wet areas in Central America. In the open forests of Guanacaste, Costa Rica, only two species have been found, both growing at the margins of rivers, while no less than 12 are reported from the rain forest in the northern part of that country.

As may be surmised, the means of dispersal preclude a rapid expansion and, despite the protective devices against drought found in the embryo, the seedlings require a clean and wet ground on which to grow. It is because flooded areas provided such a habitat that *Inga* is so common in them and also because whole fruits are frequently transported by rivers. *Inga* has not attained, however, the narrow adaptation to this habitat that occurs in some species of *Pithecellobium*. In areas where precipitation reaches a critical point for *Inga*, as in the Lesser Antilles, it is restricted to the high forests, where it becomes very successful. Its occurrence in adjacent savannas seems to be rather accidental.

The geological history of the area may help to explain the present geographic distribution. Fossils attributed to *Inga* have been found in the Cretaceous, both in Europe and North America, in Panama (Oligocene), in Costa Rica (Miocene) and in Bolivia (Pliocene). All consist of leaf impressions, and it is very difficult to assign them with certainty to *Inga* rather than to some other related genus. According to the present views on the biogeography of the area (Schuchert, Historical geology of the Antillean-Caribbean region, 106-110, 1935), it is quite possible that a migration of species from South America could have reached the Central American mainland in the upper Cretaceous. One of the most widely distributed species, *I. vera*, seems to have taken two routes of migration in Central America; one to northwestern Mexico, and the other towards the Greater Antilles; the latter were connected to the continent until the middle Miocene, which may explain the present

distribution of that species in Jamaica, the eastern tip of Cuba (introduced?), Hispaniola and Puerto Rico.

A different history occurs in the Lesser Antilles. The species found in this group of islands are markedly of Amazonian-Venezuelan origin. Of the 11 species found in Trinidad, 10 also occur in Venezuela. Two of them extend to Tobago and Martinique, while only one, *I. fagifolia,* is found farther than the Anegada passage which separates the continental shelf of the Greater Antilles from the volcanic arch extending from Anguilla to Grenada. *Inga fagifolia* is found in all the Lesser Antilles, Puerto Rico and Hispaniola but does not occur in Jamaica, an island which has been thoroughly explored. This species, of which closer allies are found in central and southern Brazil, extends to Mexico in one direction but evidently its distribution to the Lesser Antilles and Hispaniola occurred *via* the Trinidad-Venezuela connection. As for many other plants, its distribution in the Lesser Antilles and Hispaniola may be explained either by the existence of a land bridge connecting the islands, a theory that has few supporters among geologists, or through waif dispersal. Two of the endemics of the Antilles, *I. dominicensis* (Dominica) and *I. martinicensis* (Martinique, Guadeloupe), are restricted to the old nucleus of the Lesser Antilles; the third, *I. venosa,* a poorly known species, occurs in Trinidad.

Economic Importance

Although none of the species of *Inga* has a basic economic importance, they are useful in a wide variety of ways and man has paid close attention to these trees in different stages of his civilization.

Fuel wood. Since colonial times, especially in the Antilles, the different species of *Inga* have supplied a good fuel wood for domestic and industrial uses. Oviedo, in 1535, mentions this use in the first sugar mills established in America, located in Hispaniola, and centuries later Père Labat refers to the same use in the French Antilles. At present it is of considerable importance in the coffee growing areas of Central America and Colombia; these densely populated regions depend for fuel production on the wood of *Inga* trimmed off each year from the shade trees in the coffee fields. As natural supplies are scarce and the consumption high, in some places all the fuel is supplied from such trees.

Shade for cacao and coffee. One of the most interesting discoveries of pre-Columbian agriculture was the use of leguminous trees for the shade of cacao. Cacao grows naturally under the tall trees of the rain forest, and when the early Indians started its cultivation in a formal way it was probably after long experimentation that they found that leguminous trees not only furnish a good type of shade but even increase the yield of cacao. This occurred, of course, several centuries before the discovery of nitrogen fixation. The first tree so used was *Gliricidia sepium* (Jacq.) Steud.

In cultivation of coffee, the effect of shade is to lengthen the life of the plant by reducing overproduction, maintaining a high fertility rate in the soil and preventing erosion. For this purpose *Inga* trees are planted at regular intervals in the coffee plots, and by corrective pruning they attain the size and shape desired

by the planter. The use of *Inga* as shade is discussed in the standard works on coffee culture (Marrero, Caribbean Forester **51:** 54-71, 1954). Several species have been introduced into Africa (Angola) with the purpose of finding better shade trees for coffee.

For their rapid growth and the large quantities of organic matter produced *I. edulis, I. oerstediana, I. speciosissima* and others are preferred by the farmers. Very often the shade is not provided by trees of only one species, but several are planted together.

Within the genus, also, selection for the most desirable species is progressing. *Inga paterno,* once a favorite, now is almost eliminated by a witches'-broom disease that reduces its foliage considerably. In *I. densiflora* a pink fungus attacks the branchlets and seriously damages the tree. Among others, an important problem at present is to find species or varieties of higher resistance to the fungus disease and fruit flies (*Anestrepha* spp.).

Fruit. The utilization of *Inga* as fruit trees is an ancient one and probably started independently in different places. In the lower Amazon basin it was concentrated on *I. edulis* and *I. cinnamomea,* although the varieties of the former as found in Central America are scarcely edible. In southern Brazil the species used were *I. affinis, I. uraguensis* and *I. barbata.* In the higher Amazon *I. densiflora* is frequently planted and the type specimen comes from a cultivated tree. Ducke has pointed out that the plants in cultivation produce better fruits than the ones growing in the forest. Apparently selection already is advanced.

A second center of domestication is found in Peru where *I. feuillei,* the *pacay,* was widely cultivated before the Paracas culture. The trees are abundant in the coastal lowlands and evidently received much attention from the aborigines since the pods are commonly figured in the ceramics of Paracas, Chimu, etc. Of special importance was the fact that the legumes could be stored for a long period (Yacovleff & Herrera, Rev. Mus. Nac. Lima **3:** 267, 1934), and this explains how its cultivation covered more or less the same areas as the Inca Empire from Chile and Bolivia to Ecuador. *Inga feuillei* is the only species of the genus that has been planted as a fruit tree outside the natural range, in California, Polynesia, Italy, etc.

In Central America the only species that is planted for its fruit is the *jinicuil, I. jinicuil,* the cultivation of which started in Mexico, probably in the highlands of Veracruz. Fruits of this species, as well as of *I. paterno, I. densiflora* and *I. sapindoides,* are commonly seen in the markets, while the less appreciated *I. punctata, I. spectabilis,* etc., very seldom appear. Among the poorer classes in Central America another use is given to the large seeds of some species: these are cooked, cut in small pieces, and eaten with other vegetables.

As indicated before, selection has been directed to obtain larger pods and thicker arils. Further problems that have arisen are to find plants resistant to the attacks of fungi and insects. Up to now the method of selection has been the establishment of progenies of outstanding trees with subsequent dispersion of selected material.

Vernacular Names

Several names are now in common use for *Inga.* The Brazilian word *inga,* recorded first by Marcgravius and later applied to the genus by Plumier and Scopoli, is still of wide use in Brazil in an inclusive sense, followed by an adjective for specific determination, e.g. *inga cipó* (*I. edulis*), *inga peua* (*I. ruiziana*), etc. Another South American name is *pacay* or *pacae,* probably of Peruvian origin but now extending to Uruguay, as *pacay de los bañados (I. uraguensis).*

In Central America, the Antilles, and northern South America (Colombia, Venezuela) the name *guamo* or *guabo* is generally used. This word seems to have originated in the Caribbean, perhaps in Hispaniola, and it is doubtful whether its spread was pre- or post-Columbian. From the north comes the name *cuajiniquil* (in Nahuatl, "the tree with pendant pods"), which is used with various modifications from Veracruz to Costa Rica.

Within the area where the last two names are used there are local ones of restricted interest. Most of them come from Indian dialects, but some have a common use at present such as *pepeto, chalun,* and *paterno* in Guatemala and El Salvador, *chalauitl* in Mexico, etc. The name *bribri* is used in two widely separated areas: the lagoon of Chiriquí, in Panama, and the coastal zone of British Honduras. In some parts of Mexico (Sinaloa, Michoacán) the Spanish name *vainillo* is applied to some species of *Inga.* In the Lesser Antilles and Haiti they are generally called by the French name *pois-doux,* while in the British islands, "Spanish oak," recorded by Plukenet in 1641, is reserved for *I. fagifolia.*

Infrageneric Categories

The current division of *Inga* into sections and series was first established by Bentham (in Hook., Lond. Jour. Bot. **4:** 577-621, 1845) and with minor changes maintained in his later publications (Trans. Linn. Soc. **30:** 335-664, 1875; in Mart., Fl. Bras. **15:** 458-500, 1876). From the very beginning Bentham had a broad understanding of the genus and the grouping he established seems, even now, to have a certain natural basis. However, many species were put in the wrong group, which tends to obscure the natural limits of sections and series. The delimitation of series by Bentham is difficult to follow in the keys, since they are based on highly variable and overlapping characters. In 1929 Pittier tried to redefine them, with not much success, and also created two new series for § INGA based on the structure of the legumes.

In the present treatment the categories established by Bentham are followed in large part, although some modifications are introduced. His five sections, LEPTINGA, DIADEMA, BOURGONIA, PSEUDINGA and EUINGA, are reduced to three: LEPTINGA, BOURGONIA and INGA. The first of these includes the species with globose inflorescences, divided by Bentham between LEPTINGA, if the flowers were pedicellate, and DIADEMA, if sessile. The fact that the length of the pedicel is a highly variable character, even on the same specimen, is the reason for abandoning this separation. There also is no important difference between sections PSEUDINGA and INGA;

Bentham and Pittier very often placed a species in either section depending upon the adequacy of material available (see *I. sapindoides*).

Section BOURGONIA is the most natural group among those established by Bentham and is the one that has suffered fewest transfers. On the basis of morphology alone it seems to be a rather primitive group evidently related to *Pithecellobium.* The species here are clearly defined in Central America and the West Indies, but in southern Brazil and Paraguay wide variability has been observed. The small and almost glabrous flowers with campanulate calyx are arranged in long, loose spikes, as in *I. fagifolia,* or on congested and short rhachises, as in *I. pezizifera.* The group has wide distribution, and Central America offers only two endemics: *I. longispica,* allied to the *I. coruscans* complex, more developed in Colombia than elsewhere, and the dubious *I. belicensis,* related to *I. fagifolia,* although several important characters maintain its individuality.

No clear relations can be established between § BOURGONIA and the other two sections. This is not extraordinary within the tropical *Leguminosae,* where genera are established by uniting groups of morphologically allied species of suspected polyphyletic origin.

Section INGA are a vast assemblage of intergrading groups of species held together by the possession of well developed, more or less pubescent flowers. In a total evaluation of the genus this section may acquire a subgeneric status and probably the present series could be considered as sections. As will be seen under TAXONOMY, the present treatment offers a redefinition of the series of Bentham and Pittier. The ser. GYMNOPODAE and PILOSIUSCULAE have been split in the present treatment into smaller and more natural units. The former were a vast assemblage of very different groups of species held together and differentiated by one character, the presence or absence of wings on the rhachis. As mentioned before, this is a very unstable character even in the same individual. The new series, although established in the area under study on a fraction of the total number of species, are all of them well represented in South America. The series PUNCTATAE seems to have some relation with § BOURGONIA, while the ser. PILOSULAE form a transition to the large flowered species of the subsequent series. The ser. CALOCEPHALAE of Bentham and Pittier have been divided into four independent series, one of them restricted to Central America. At the same time a revaluation of ser. TETRAGONAE has been necessary; this series, created by Pittier, includes in the present treatment some species ascribed previously to the ser. CALOCEPHALAE. By faulty correlation of legume and flower character, the same species might be classified by Bentham or by Pittier as one of the § PSEUDINGA-ser. CALOCEPHALAE if the specimen were in flower, or one of the § EUINGA-ser. TETRAGONAE if it were in fruit. The use of the latter name is maintained and the ser. CALOCEPHALAE are restricted to a South American group centered around *I. macrophylla* and *I. fastuosa* and represented in Central America only by *I. mucuna* and in the West Indies by *I. venosa,* endemic to Trinidad.

Section LEPTINGA is represented in Central America by nine species, one of which also occurs in Trinidad; in the rest of the West Indies there is none. This section is an assemblage of morphologically different species held together by one

common character, the spherical or clavate structure of the floral receptacle, giving an umbellate or globose appearance to the inflorescence. As mentioned before, this floral arrangement is probably the result of a contraction of the spikes or racemes and may be reached independently in different groups of species. This is corroborated by the trend, observed in some species of the ser. PILOSIUSCULAE, towards a condensation of the floral rhachis, as *I. venusta, I. hayesii* and especially the *I. acuminata* complex.

Of special interest in Central America is the presence of a group including *I. jinicuil, I. paterno* and *I. mortoniana,* without close affinities in neighboring areas but evidently related to the Amazonian *I. cinnamomea, I. cordistipula,* etc. Two other species are noteworthy from the morphological standpoint: *I. saffordiana,* with a particular flower structure not found in any other species in the genus, and *I. portobellensis,* in which the size and shape of the floral parts produce the most outstanding inflorescence in *Inga;* this species has some distant allies in South America (*e.g. I. inflata* Ducke.)

Section LEPTINGA is considered, then, more as a horizontal polyphyletic stage than as a group of naturally related species having a common origin. This is true of the section as a whole, but evidently within it clusters of species with strong natural affinity may be discerned. With the exception of the one about *I. jinicuil* no other complex occurs in the area in study. The other species in the section have close affinities in South America.

SPECIATION

In the delimitation of species in this genus, one is confronted with the situation that some are clearly defined entities, while in others the overlapping of taxonomic characters make an acceptable definition almost impossible. Among the first group, *I. fagifolia, I. punctata, I. thibaudiana,* and a few others present a minimal variability in spite of their large areas of distribution. The reverse is true, especially in the ser. INGA and PILOSIUSCULAE, where species are formed by clusters of populations, each with a certain morphological type but clearly intergrading towards other intraspecific groups. In the past, it has been common to give these variants specific rank, but as more material becomes available, it has been possible to fill the intergrading spaces. In some cases the group variation has a clear distribution pattern and shows marked clines, but in others the aberrant characters appear with no geographic correlation, scattered throughout the whole range of distribution. Thus the variant called *I. fissicalyx* Pittier, with elongate stipules, sepals and leaves, occurs among otherwise typical populations of *I. vera* in widely separated parts of Mexico and Costa Rica.

Of the dilemma of raising to specific level all the possible variants and increasing the names *ad infinitum,* or considering them as minor variants within a species, the second has been preferred for this study. Some of the most important groups of variants are discussed as infraspecific entities without attempting any nomenclatorial definition.

The factors that have produced the striking variability in *Inga* are unknown. It has been suggested that hybridization is important, and this is possibly true in the

species cultivated as shade trees where different populations are planted together and then reproduced by mixed progenies. On the other hand, there are some factors that operate in reducing the effectiveness of hybridization, such as the type of pollination, seasonal isolation, and in natural populations the restricted dispersal.

Climatic and edaphic factors may have contributed considerably to the formation of infraspecific groups. Species such as *I. oerstediana,* which grows from sea level to almost 2,000 m elevation in Colombia and Central America, show such different types between the coastal and mountain populations that these have received different common names. However, they have many characters in common and the intergrading phases occur in the intermediate areas.

Geographical isolation in terms of geological periods is also very important. In *I. vera*, for example, the populations in the greater Antilles have been isolated from the bulk of the species probably since the late Miocene and offer quite a number of separating characters. The same occurs in the semi-arid areas of northern and central Mexico, where this species clearly shows subspecific differentiation.

There is no information on mutation patterns in *Inga*. However, observation of large populations, such as are found in coffee fields, reveals a remarkable polymorphism which is difficult to attribute to segregation alone. The accompanying illustration of three types of leaves of *I. edulis* shows a common pattern of variation (Fig. 1).

The human factor has been very important in speciation. Types cultivated

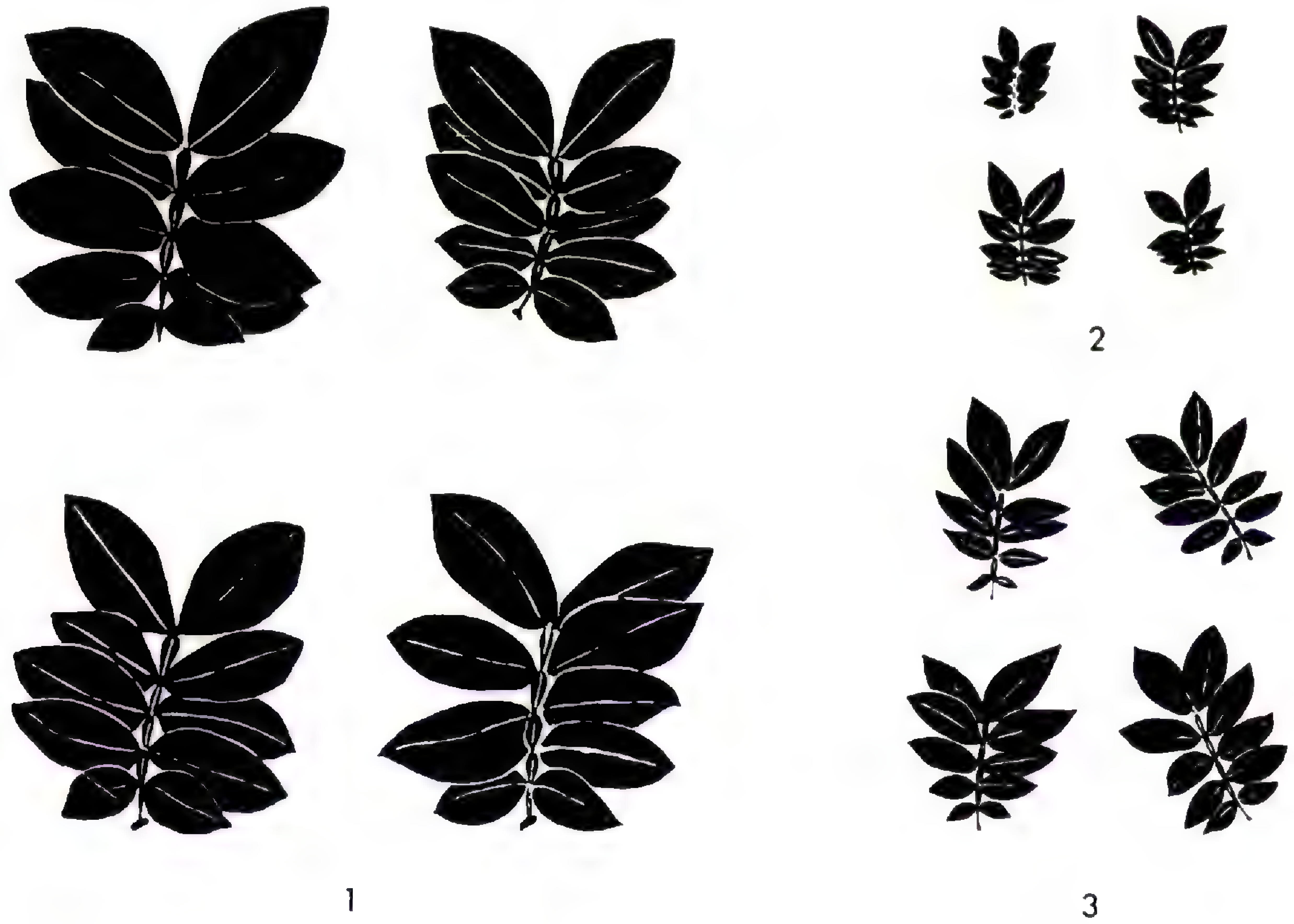


Fig. 1. Variation in a population of *Inga edulis* Mart.; representative leaves of three trees grown for shade in the same coffee grove. × 4.

as fruit trees or for shade have been selected, introduced into new areas, and may have contributed to the formation of new variants through hybridization.

Endemism is particularly important in four areas: the highlands of Mexico, the mountains of Costa Rica and the coastal lowlands of Panama; another center in the Lesser Antilles occupies the oldest section of the volcanic arch, from Martinique to Dominica. The endemics of Costa Rica, Panama, and the Caribbean islands show more affinities with South American species, while in the Mexican endemics this relationship is less marked. No one of the four centers already mentioned could be compared in number and variability of species with the Amazon basin or the Colombian cordilleras.

Study Material

For the preparation of this study materials of the following herbaria were consulted: B, CR, EAP, F, GH, IAIAS, ILL, K, MO, NY, RB, US and VEN. I wish to acknowledge my indebtedness to the curators of the herbaria mentioned, and particularly to the Director and Staff of the Missouri Botanical Garden, where this work was completed.

Taxonomy

Inga [Plum.] Scop., Introd. Hist. Nat. 298, 1777; Willd. in L., Sp. Pl. **4:** 1012, 1806; DC., Prodr. **2:** 432, 1825; Benth. in Hook., Lond. Jour. Bot. **4:** 577, 1845; Benth., Trans. Linn. Soc. **30:** 601, 1875; Pittier, Contr. U. S. Nat. Herb. **18:** 173, 1916; Pittier, Jour. Dept. Agr. Porto Rico **13:** 117, 1929.

Amosa Neck., Elem. **2:** 459, 1790.
Torealia Nor., Verh. Batay. Gen. **5,** Art. IV. 4, 1790.
Ingaria Raf., Sylva Tell. 119, 1838.
Feuilleea O. Ktze., Rev. Gen. Pl. **1:** 182, 1891 (pro parte).

Trees; branchlets glabrous or pubescent, lenticellate in age. *Leaves* alternate, once-pinnate; leaflets opposite, in 2 to many pairs, the terminal largest, the petiolules very short; rhachis terete or winged, ending in a linear, caducous appendage, the nectarial glands always present at the insertion of the leaflets; petiole terete or winged, with a clearly marked pulvinus; stipules small to large, generally caducous. *Inflorescences* axillary or terminal, 1 to ∞, fasciculate or paniculate; peduncle elongate to obsolete; rhachis elongate to condensed in a spheric or clavate structure, the bracts small or large, caducous or persistent. *Flowers* sessile to pedicellate, regular, white or yellow; calyx minute to very large, campanulate to tubular, synsepalous, the 5 segments regular or unequal, valvate in bud; corolla tubular to funnelform, sympetalous, 5-lobed, usually appressed-pilose; stamens numerous, the filaments united below, free above, included or exserted, the anthers eglandular, the pollen in massulae; gynoecium 1-carpellate, the ovary elongate, glabrous or pubescent, the style generally longer than the filaments, the stigma simple or lobed. *Legume* flat, quadragonal, or subterete, the margins narrower or wider than the valves, irregularly dehiscent; seeds oblong, covered by a loose, succulent aril, the cotyledons coriaceous.

Type species: *Inga vera* Willd.

Key to the Sections (I-III) and Series (1-13)

a. Inflorescence racemose.

b. Calyx minute, less than 2 mm long, glabrous or very sparsely pubescent; legume flat, glabrous .... I. BOURGONIA (p. 281)

bb. Calyx well developed, more than 2 mm long, pubescent or glabrate; legume flat, tetragonal or subterete .... II. INGA (p. 289)

c. Legume flat with narrow margins, or tetragonal with the margins and valvular sides more or less equally broad.

d. Corolla less than 15 mm long (except in *I. multijuga* and *I. skutchii*), always less than 3 mm wide.

e. Calyx regular, the teeth of the same size (except in *I. skutchii* and *I. pinetorum*).

f. Calyx pilose to glabrescent; rhachis winged, marginate or terete; glands patelliform; bracts short and broad.

g. Leaflets 2-4 pairs; rhachis terete .... 1. PUNCTATAE (p. 289)

gg. Leaflets 4-10 pairs; rhachis winged, terete or marginate.

h. Leaflets 5-8 pairs; rhachis terete; corolla more than 10 mm long (except in *I. ruiziana* .... 2. MULTIJUGAE (p. 297)

hh. Leaflets 5 or less pairs; rhachis winged or marginate; corolla less than 10 mm long .... 3. DENSIFLORAE (p. 302)

ff. Calyx setose, the teeth subulate; rhachis winged; glands stipitate; bracts narrow, lanceolate .... 4. LEPTANTHAE (p. 312)

ee. Calyx markedly cleft on 1 or 2 sides

i. Flowers small, corolla less than 12 mm long, congested in a very short spike; plant glabrous .... 5. ACUMINATAE (p. 313)

ii. Flowers relatively large, corolla more than 12 mm long, in loose spikes; leaves and flowers yellow-pilose .... 6. PILOSULAE (p. 314)

dd. Corolla more than 15 mm long, or if less, then more than 3 mm wide

j. Calyx more than 15 mm long; legume densely ferrugineous-pubescent.

k. Calyx narrow, less than 5 mm wide, more than 17 mm long .... 7. CALOCEPHALAE (p. 317)

kk. Calyx broad, 8-12 mm wide, less than 17 mm long .... 8. GOLDMANIANAE (p. 319)

jj. Calyx less than 15 mm long.

l. Calyx cupular, densely lanose; rhachis terete (in the Central American species) or winged; flowers distant, often pedicellate; bracts caducous .... 9. DYSANTHAE (p. 320)

ll. Calyx tubular, pilose or glabrescent; rhachis generally winged; flowers congested; bracts persistent or subpersistent.
 m. Legume flat.
  n. Leaves and branchlets glabrous or sparsely pilose; glands short, patelliform; legume thick, 30-70 cm long ....10. SPECTABILES (p. 322)
  nn. Leaves and branchlets densely yellow or ferrugineous-pilose, in age glabrous; glands thin, long-stipitate; legume thin, less than 30 cm long ....11. VULPINAE (p. 323)
 mm. Legume tetragonal ....12. TETRAGONAE (p. 324)

cc. Legume subterete, the valvular sides reduced and narrower than the margins, sulcate ....13. INGA (p. 328)

aa. Inflorescence capituliform or umbelliform; flowers small, glabrous or tomentose, legume flat ....III. § LEPTINGA (p. 344)

SECTION I. BOURGONIA Benth. in Hook., Lond. Jour. Bot. **4:** 585, 1845 (as *Burgonia*).

Flowers minute, glabrous or sparsely pubescent, sessile or very shortly pedicellate, in rather loose inflorescences; calyx campanulate, less than 2 mm long; corolla tubular-funnelform, 3-4 times longer than the calyx. *Inflorescences* with peduncle shorter or longer than the rhachis, in the first case as long cylindric spikes, in the latter as ovoid to oblong spikes or racemes. *Legume* flat, glabrous, with prominent margins. Leaves glabrous or very sparsely pubescent, the lateral nerves distant, the rhachis terete, marginate or narrowly winged. *Trees* with dense crown and rather shallow root system. SPECIES . . . 1-6.

a. Floral rhachis longer than the peduncle; inflorescence cylindric, lax, 4-8 cm long.
 b. Foliar rhachis winged or marginate ....1. I. MARGINATA
 bb. Foliar rhachis not winged, sometimes scarcely marginate.
  c. Spikes about 17 cm long. Costa Rica ....2. I. LONGISPICA
  cc. Spikes less than 15 cm long.
   d. Leaflets generally in 2-3 pairs, the upper pair less than 16 cm long; stipules minute. Mexico to Panama ....3. I. FAGIFOLIA
   dd. Leaflets in 3 pairs, the upper pair more than 16 cm long; stipules conspicuous. Panama ....4. I. CORUSCANS

aa. Floral rhachis shorter than the peduncle; inflorescence conic, congested, 1-2 cm long.
 e. Foliar rhachis winged or marginate; upper leaflets less than 12 cm long. British Honduras ....5. I. BELICENSIS
 ee. Foliar rhachis terete; upper leaflets more than 15 cm long. Panama ....6. I. PEZIZIFERA

1. INGA MARGINATA Willd. in L., Sp. Pl. **4:** 1015, 1806. (Type *Bredemeyer s.n.* photo)

Inga sapida H.B.K., Nov. Gen. Sp. Pl. **6:** 286, 1824, non Benth. (ex char.; Type *Humboldt & Bonpland s.n.*, not seen)
Mimosa semialata Vell., Fl. Flum. 11: *t. 5,* 1835. (ex ic.)

Inga guayaquilensis G. Don, Gen. Hist. Dichl. Pl. **2:** 391, 1832 (*fide* Bentham). (Type *Ruiz & Pavon s.n.*, not seen)
I. odorata G. Don, loc. cit. 388 (*fide* Bentham). (Type *Ruiz & Pavon s.n.*, not seen)
I. semialata (Vell.) Mart., Flora **20,** Bd. 2 Beibl. 111, 1837.
I. excelsa Poeppig, Nov. Gen. Sp. Pl. **3:** 78, 1845 (*fide* Bentham). (Type *Poeppig s.n.*, not seen)
I. puberula Benth. in Hook., Lond. Jour. Bot. **4:** 589, 1845 (*fide* Bentham). (Type *Pohl s.n.*, not seen)
I. pycnostachya Benth., loc. cit. (Type *Matthews s.n.*, not seen)
Feuilleea marginata (Willd.) O. Ktze., Rev. Gen. Pl. **1:** 188, 1891.

Trees up to 20 m tall, the crown dense and spreading; branchlets terete, glabrous, lenticellate. *Leaves* with 2 pairs of leaflets; leaflets elliptic to falciform, acute to long-acuminate at the apex, the base acute and strongly asymmetric, above dark green, lustrous, glabrous to sparsely pilose, the 4-6 pairs of lateral nerves distant and prominent, beneath glabrous, the nerves prominent, the upper pair narrowly elliptic to falciform, 7-14 cm long, 2.5-5.0 cm wide, the lower pair elliptic, 4-9 cm long, 1.5-4.0 cm wide; the petiolules up to 3 mm long, densely pilose; rhachis cuneately winged to marginate, 2-4 cm long, glabrous, the glands patelliform, less than 1.5 mm wide; petiole winged or marginate, 1.0-2.5 cm long, the pulvinus terete and dark, about 0.5 cm long, minutely pilose; stipules lanceolate, up to 5 mm long, striate, pubescent, caducous. *Inflorescences* 1-4, axillary; peduncle terete, 0.5-3.0 cm long, densely pubescent to glabrous; rhachis 4-11 cm long, the bracts linear, 2 mm long, persistent. *Flowers* distant or congested, sessile to pedicellate, the pedicels up to 3 mm long; calyx minute, campanulate, about 1 mm long, pilose at the base, glabrescent above, the teeth acute and more pubescent; corolla 3 mm long, narrowly tubular in the lower third, funnelform above, glabrous below, the lobes short, pilose; staminal tube exserted. *Legume* flat, oblong, deeply constricted between the seeds, up to 14 cm long and 1.5 cm wide, glabrous.

Common in the wet forests at below 800 m elevation. Costa Rica and Panama. (Widely distributed in South America, extending to Brazil and Bolivia.)

Vernacular name: *cuajiniquil negro* (Costa Rica).

COSTA RICA: ALAJUELA: La Tigra, San Carlos, *Barquero 14* (IAIAS, MO); Pata de Gallo, San Ramón, *Brenes 6589* (F), *Brenes 6646* (F), Santiago de San Ramón, *Brenes 6689* (F). CARTAGO: Atirro, *J. D. Smith 6493* (GH, NY, US); Las Vueltas, Tucurrique, *Tonduz 12744* (CR); Tuis, *Tonduz 11349* (NY, US); Turrialba, *Gregory 1881* (IAIAS), *Holdridge 2475* (IAIAS), *de Wolf 175* (IAIAS), GUANACASTE: Laguna Arenal, *Brenes 12657* (F); Naranjos Agrios, *Standley & Valerio 46387* (F, US); Nicoya, *M. Valerio 501* (CR, F); Quebrada Serena, *Standley & Valerio 46077* (F, US); Tilarán, *J. Valerio 51* (US). HEREDIA: Puente de Mulas, *Echeverria 347* (CR, F), *Sáenz 61* (CR, F). LIMON: Jiménez, *J. J. Cooper 10198* (US); Montecristo, *Standley & Valerio 48645* (F); Sipurio, *Tonduz 8710* (CR, F, GH, US); Siquirres, *Lankester 948* (US). PUNTARENAS: Buenos Aires, *Tonduz 6690* (F, US); Golfito, *Allen 6242* (EAP). SAN JOSE: Aserrí, *León 3838* (IAIAS, MO); El General, *Skutch 4111* (MO, NY, US), *Skutch 4288* (MO, NY).

PANAMA: BOCAS DEL TORO: Almirante, Daytonia Farm, *Cooper 546* (F); Changuinola Valley, *Dunlap 282* (US), *Seibert 1582* (MO); Chiriqui Lagoon, *von Wedel 1378* (GH, MO, US); Water Valley, Chiriqui Lagoon, *von Wedel 1549* (GH), *1807* (GH, MO, US). CANAL ZONE: Barro Colorado Island, *Bangham 535* (F), *Shattuck 516* (F), *Standley 40996* (US), *Woodworth & Vestal 610* (F), *Zetek 3824* (F), *4322* (F); Gatún, *Pittier 6512* (GH, NY, US); without locality, *Hayes 950* (NY). COCLE: Valle de Antón, *Allen 2231* (F, MO, US). DARIEN: Sambú River, *Pittier 5579* (US).

The Central American material of *I. marginata* shows very slight variability; all the leaves are bijugate, with one exception, and offer a remarkable similarity in shape and structure; the indument varies from none to a short and dense pubescence on the costa and main nerves. In contrast the variability in South America is very high, especially in Brazil and Paraguay. Its relation to *I. cylindrica* (Vell.) Mart. is not clear and many of the published varieties also are of dubious standing.

In Central America *I. marginata* is commonly planted as a shade tree in the coffee fields, although the dense crown and the superficial root system hardly make it desirable.

2. Inga longispica Standley, Publ. Field Mus. Nat. Hist., Bot. Ser., **18:** 497, 1937. (Type *Brenes 6371*)

Trees; branchlets terete, striate, glabrous, densely lenticellate. *Leaves* with 3 pairs of leaflets; leaflets subcoriaceous, elliptic to lanceolate-oblong, the apex acuminate, the acumen 0.5-1.0 cm long, mucronate, the base acute, decurrent, above dark green, lustrous, glabrous except for a sparse pilosity on the costa, punctate, the 6-8 pairs of lateral nerves slightly prominent or sunken, beneath paler, glabrous, the nerves prominent, the tertiary nervation conspicuous and finely reticulate, the upper pair elliptic, oblique, 6-11 cm long, 2-4 cm wide, the medium and lower pairs lanceolate-elliptic, the lowermost 3-5 cm long, 1.0-2.5 cm wide, the petiolules 1-2 mm long, pilose; rhachis terete, caniculate above, 4-6 cm long, sparsely pilose, the glands small, stipitate, pertuse; petiole terete, 1.0-1.5 cm long, glabrous, the pulvinus about one third of the length, darker and thicker. *Inflorescences* axillary, often at the defoliated nodes; peduncle 3-6 cm long, striate, papillose; rhachis 8-13 cm long, the bracts minute, deciduous. *Flowers* distant, sessile; calyx campanulate, about 2 mm long, sparsely pilose, the teeth obtuse; corolla tubular-funnelform, 5-6 mm long, sparsely pilose, the lobes acute, about 2 mm long, sometimes retroflexed; staminal tube included, the filaments 1.5-2.0 cm long. *Legume* unknown.

Wet forests of central Costa Rica, at 1000-1200 m elevation.

Costa Rica: alajuela: La Palma, San Ramón, *Brenes 6371* (CR, F, IAIAS); Vara Blanca, *Skutch 3705* (MO, NY, US). san jose: La Palma de Coronado, *Holdridge 5948* (IAIAS).

An isolated species remarkable for the long spikes and short, sessile flowers. It seems related to *I. coruscans* H.B.K. in the general habit, differing however in the structure of the inflorescence and the size and shape of the leaflets.

3. Inga fagifolia (L.) Willd. ex Benth., Trans. Linn. Soc. **30:** 607, 1875.—Fig. 2.

Mimosa fagifolia L., Sp. Pl. 516, 1753 (Based on Pluk., Alm. *t. 241, fig 21*), non Jacq. (1763).
M. laurina Sw., Prodr. 85, 1788. (ex char.) (Type *Masson s.n.*, not seen)
Inga laurina (Sw.) Willd. in L., Sp. Pl. **4:** 1018, 1806.
Mimosa tetraphylla Vell., Fl. Flum. **11:** *t. 8,* 1827. (ex ic.)
Inga tetraphylla (Vell.) Mart., Flora **20:** Beibl. 112, 1837.
Feuilleea laurina (Sw.) O. Ktze., Rev. Gen. Pl. **1:** 184, 1891.
F. fagifolia (L.) O. Ktze., loc. cit. 187.

Trees with dense crown; branchlets terete, gray or whitish, glabrous, striate, lenticellate. *Leaves* relatively small, with 2-3 pairs of leaflets; leaflets coriaceous, obovate to narrowly elliptic, often very asymmetric, rounded, broadly acuminate or retuse at the apex, the base acute, unequal, above deep green, lustrous, glabrous, with 5-7 pairs of prominent nerves, the reticulate nervation conspicuous, beneath paler, glabrous, the nerves prominent, the upper pair elliptic to obovate, 4-16 cm long, 2-6 cm wide, the lower pair 3-9 cm long, 1-4 cm wide; rhachis terete or

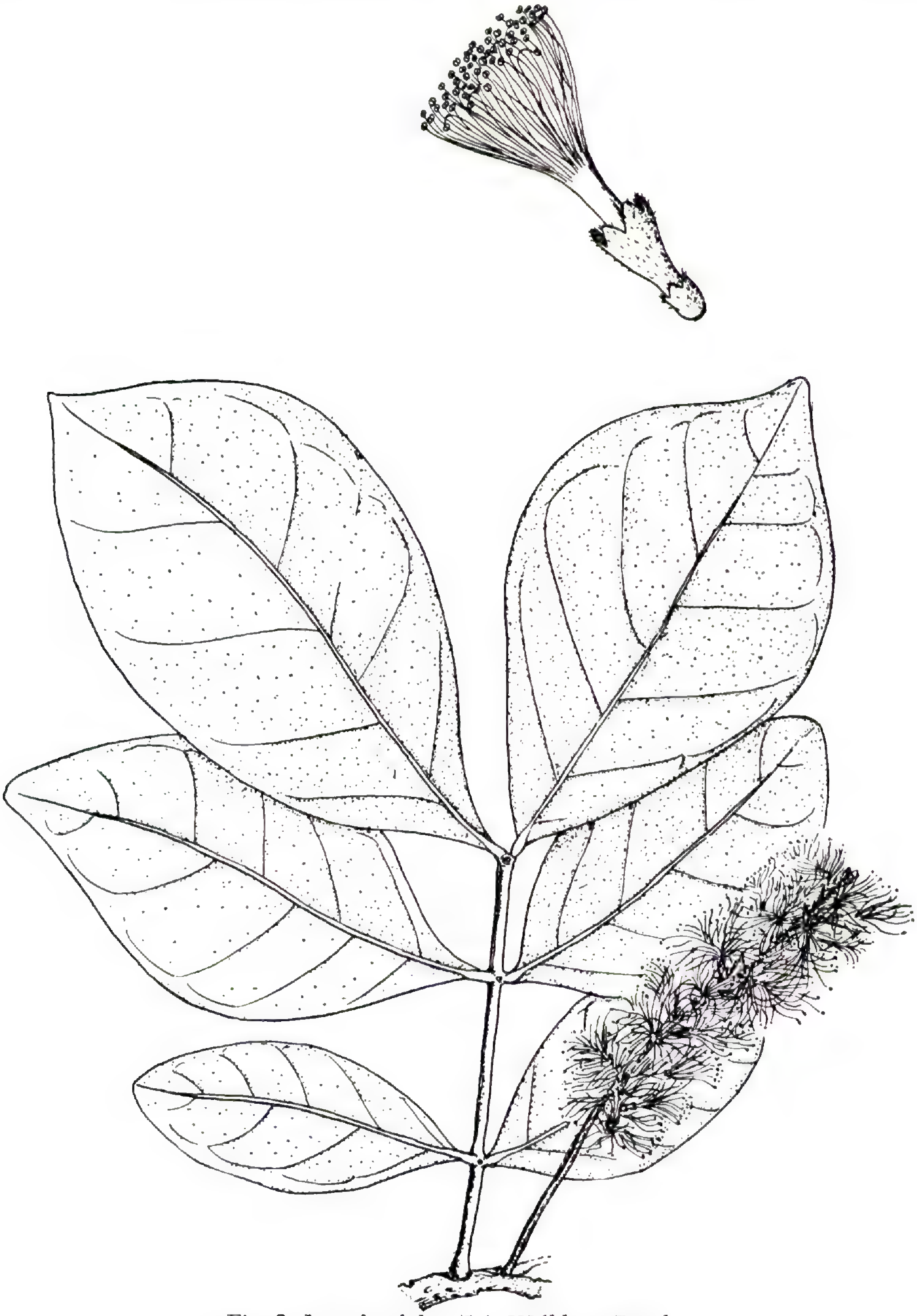


Fig. 2. *Inga fagifolia* (L.) Willd. ex Benth.

marginate, with a groove in the upper side, 2-6 cm long, glabrous or sparsely pilose, the glands patelliform, short-stipitate, less than 1 mm in diam; petiole terete, 1.0-2.5 cm long, sulcate above, minutely pubescent to glabrous, the pulvinus thick and dark; stipules oblong, up to 7 mm long, 4 mm wide, glabrous or pubescent at the round apex, thick and persistent. *Inflorescences* axillary, 1-5 spikes in the same axil, congested in the terminal branchlets; peduncle terete, 1-4 cm long, striate, glabrous or sparsely pilose; rhachis angulate, 3-11 cm long, glabrous or rarely sparsely pilose. *Flowers* sessile, in rather loose spikes; calyx tubular, 1-2 mm long, striate, glabrous or sparsely pilose, the teeth shallow, pubescent at the tips; corolla funnelform, the throat about half the total length, 3-6 mm long, glabrous or sparsely pilose, the lobes acute, not spreading, about 1 mm long, pubescent at the apex; staminal tube included to long-exserted, the filaments up to 12 mm long. *Legume* flat, oblong, 10-30 cm long, 2-5 cm wide, transversely striate, glabrous, the borders not markedly elevated.

Wet to semi-dry forests, or highland savannas. Mexico to Panama; Haiti to Trinidad. (South America.)

Vernacular names: *caspiro, nacaspiro* (Guatemala-Standley); *paternillo* (El Salvador-Calderón); *jina* (Dominican Republic-Valeur); "*Spanish oak*" (Lesser Antilles).

MEXICO: CHIAPAS: Escuintla, *Matuda 46* (MO, NY, US), *1862* (F, K, US). GUERRERO: Acapulco, *Palmer 584* (F, GH, K, MO, NY, US). JALISCO: Hacienda San Marcos, *Pringle 5494* (GH). NAYARIT: Ixtapa, *Nelson 4149* (US); Tepic, *González Ortega 43* (US). OAXACA: Tuxtepec, Chiltepec, *Martínez-Calderón 171* (US).

GUATEMALA: ALTA VERAPAZ: Sepacuité, *Cook & Griggs 760* (US), *761* (US). ESCUINTLA: Escuintla, *J. D. Smith 2825* (US), *Hayes s.n.* (GH); *Rio Burrión*, NE of Escuintla, *Standley 89578* (F, US); without locality, *Aguilar 1685* (F). IZABEL: Quiriguá, *Standley 24253* (US). RETALHULEU: Retalhuleu, *Standley 88829* (F); Retalhuleu to Asintal, *Standley 87808* (F); Nueva Linda, *Standley 87254* (F), *87304* (F). SUCHITEPEQUEZ: Mazatenango, Las Animas, *Maxon & Hay 3451* (NY, US).

EL SALVADOR: AHUACHAPAN: Ahuachapán, *Standley & Padilla 2836* (F). LA PAZ: Zacatecoluca, *Calderón 293* (GH, NY, US). SAN SALVADOR: Tonacotepeque, *Calderón 215* (GH, NY, US), *Standley 19450* (GH, NY, US). SAN VICENTE: San Vicente, *Standley 21744* (F, GH, MO, NY, US). SONSONATE: Juayúa, *Pittier 1990* (US).

NICARAGUA: ZELAYA: El Recreo, *Standley 19812* (F).

COSTA RICA: CARTAGO: Las Vueltas, Tucurrique, *Tonduz 12991* (US), *León 3001* (IAIAS).

PANAMA: CANAL ZONE: Barro Colorado Island, *Bangham 547* (F), *M. Brown 65* (F), *Shattuck 797* (F), *Wettmore & Abbe 129* (F, GH), *Zetek 4356* (F). CHIRIQUI: Boca Chica, Horconcitos, *Pittier 5119* (GH, NY, US), *Seemann 1689* (GH). COCLE: Penonomé, *R. S. Williams 532* (NY, US). HERRERA: Ocú, *Allen 4037* (F, MO). PANAMA: Capira, *Allen 1688* (GH, NY, US); El Cermeño, *Zetek 4403* (F, MO, NY); Río Pacora, *Allen 817* (F, GH, MO, US); Río Tapia, *Standley 30673* (US).

HAITI: SUD: Carbajel to Bois-Charles, *Ekman 6063* (US); Morne Baymond, *Christ 2092* (US).

DOMINICAN REPUBLIC: ALTA GRACIA: Higüey, *Taylor 417* (NY). DUARTE: San Francisco de Macorís, *Abbot 2212* (US). LA VEGA: Contanza, *Tuerckheim 3300* (F, GH, MO, NY, US). MACORIS: Consuelo, *Taylor 326* (F, NY). MONTE CRISTI: Monción, *Mera* (*Herb. Jim. 2089*) (US), *Valeur 716* (F, MO, NY, US). PACIFICADOR: Pimentel, *Abbot 636* (US). SAMANA: Samaná, *Muller s.n.* (US); Sánchez, *Abbot 2733* (US). SEIBO: Azui, *Taylor 291* (F, NY). WITHOUT LOCALITY: *Scarff 18a* (F), *Wright, Parry & Brummel 75* (GH, US), *86* (F).

PUERTO RICO: AGUADILLA: Maricao, *Otero & Alvarez 550* (F, MO). ARECIBO: Utuado, *Sargent 109* (US), *Sintenis 6504* (F, GH, MO, NY, US). MAYAGUEZ: Cabo Rojo, *Sintenis*

724 (GH, US); Las Mesas, *Holm 271* (GH); Mayagüez, *Britton & Marble 589* (US), *Cowell 555* (NY), *Heller 4376* (F, MO, NY), *Miller 1635* (US); Sabana Grande, *Sargent 464* (US); San Sebastián, *Sargent 228* (US). GUAYAMA: Barranquitas, *Britton & Britton 8827* (NY, US); Caguas, *Heller 925* (F, NY, US); Sierra de Naguabo, *Shafer 3198* (NY, US). HUMACAO: Sierra de Yabucoa, *Sintenis 2607* (US). PONCE: Coamo, El Tendal, *Britton, Britton & Brown 6022* (NY); Coamo Springs, *Underwood & Griggs 514* (NY, US); Ponce, *Britton & Shafer 1741* (NY, US); Ponce to Coamo, *Heller 508* (F, NY, US). SAN JUAN: Bayamón, *Stahl 384* (US); Río Piedras, *Goll, Cook & Collins 302* (NY, US), *J. R. Johnston 581* (NY), *Bro. Hiram s. n.* (NY), *Stevenson 241* (US), *581* (US), *2467* (NY, US). VIEQUEZ ISLAND: Isabel Segunda, *Shafer 2490* (NY, US); without locality, *Blaner 186* (NY). PROVINCE UNKNOWN: Monte Torrecilla, *Britton, Cowell & Brown 5609* (NY). WITHOUT LOCALITY: *Kuntze 465* (NY), *Sessé, Mociño, etc. 3785* (F).

VIRGEN GORDA: Forests, *Fishlock 309* (NY).

TORTOLA: Town to High Bash, *Britton & Shafer 716* (F, NY, US).

ST. JUAN: Bordeaux, *Britton & Shafer 561* (NY, US).

ST. THOMAS: Signalhill, *Eggers s. n.* (US); St. Peter, *Britton & Marble 1226* (F, NY, US); without locality, *Eggers 264* (GH).

ST. CROIX: Mt. Eagle, *Thompson 429* (NY); without locality, *Bertero s. n.* (MO).

SABA: without locality, *Bolding 1578* (NY).

ST. KITTS: Wingfield Estate, *Britton & Cowell 484* (NY, US).

ANTIGUA: Donning Valley, *Box 1031* (US); without locality, *Rose, Fitch & Russell 3457* (F, GH, MO, NY, US).

MONTSERRAT: Soufrière, *Shafer 587* (F, NY, US).

GUADELOUPE: Bailliff, *Stehlé 280* (US); Ile de Saints, *Stehlé 92* (NY); Point-a-Pitre, *Stehlé 237* (NY); without locality, *Questel 2637* (US), *Duss 2633* (NY, US).

DOMINICA: Hampstead, *F. E. Lloyd 655* (NY); Lisdara Estate, *G. P. Cooper 185* (F, GH, NY, US); St. Acomant, *F. E. Lloyd 564* (NY); Sylvania Estate, *Hodge 611* (NY, US).

MARTINIQUE: Macouba, *Hahn 436* (GH); Parnasse, *Duss 1157* (NY, US); Rivière de la Case Pilote, *Hahn 1169* (US); Rivière Mme. Tivoli, *Stehlé 5690* (F, US); without locality, *Fairchild s. n.* (US), Sieber's *distr. Fl. Mart. 324* (GH, MO).

BARBADOS: Dodds, St. Philip, *Bot. Sta. Herb. Barbados 418* (F, GH, NY); without locality, *Waby 105* (F).

ST. VINCENT: Windsor Forest, *J. S. Beard 231* (MO); without locality, *Smith & Smith 677* (GH, NY), *1047* (NY), 1912 (GH).

GRENADA: Les Avocats, St. David's, *Broadway s. n.* (GH, MO, NY, US); Grand Etang, *Sterring 293* (US).

TRINIDAD: without locality, *Sieber 120* (GH, MO); *Trin. Bot. Gard. Herb. 1410* (US).

Inga fagifolia is one of the species with more ample geographic distribution within the genus, extending from Jalisco to southern Brazil. It is also one of the few species of *Inga* that do well in rather dry climates; its habitat, however, ranges from the dry scrublands in some Caribbean islands to the rain forest or the wet cloudy forests of the Central American highlands. A remarkable morphological variability, as expected, is found throughout the range: 1) From Mexico to Panama, 3-jugate leaved specimens predominate, as well as large fruits. 2) In the Antilles the species extends from Hispaniola to Trinidad, showing a recent relation between the continental bloc of the Greater Antilles and the volcanic islands of the Lesser Antilles; here the specimens show bijugate leaves, small and thick fruits, but in other vegetative characters as well as in the flower structure they are much like the Central American plants.

Although the original name *M. fagifolia* was given to a West Indian plant (from Plukenet's *Almagestum* giving the locality as Barbados), *I. fagifolia* in recent times has been applied to the Brazilian plants, using the name *I. laurina* for the Central American and Antillean plants. After examining many specimens,

some of them mentioned by Bentham, it seems that the differential characters between the two, such as the length of the staminal tube, are so variable within the same specimens or in small areas (including some in Central America), that they do not justify a specific segregation.

4. INGA CORUSCANS Willd. in L., Sp. Pl. **4:** 1017, 1806. (Type *Bonpland s.n.* photo)

Mimosa coruscans (Willd.) Poir. in Lam., Encycl. Suppl. **1:** 43, 1810.
Feuilleea coruscans (Willd.) O. Ktze., Rev. Gen. Pl. **1:** 87, 1891.
Inga caldasiana Britton & Killip, Ann. N. Y. Acad. Sci. **35:** 115, 1936. (Type *Mutis* 3539)

Trees up to 20 m tall; branchlets terete, glabrous, lenticellate. *Leaves* with 3 pairs of leaflets; leaflets coriaceous or chartaceous, elliptic to lanceolate, the apex obtuse to broadly apiculate, the base acute or obtuse, above lustrous and glabrous, the 6-10 lateral nerves distant and impressed, with tertiary nervation conspicuous, beneath glabrous, the nerves markedly prominent, the upper pair elliptic to obovate, 15-17 cm long, 6-7 cm wide, the intermediate pair elliptic, 10-14 cm long, 3-6 cm wide, the basal pair oblong to lanceolate-oblong, about 9 cm long, 4 cm wide, the petiolules thick and dark, about 3 mm long; rhachis terete to slightly marginate, 6-10 cm long, glabrous, the glands patelliform, about 2 mm in diam; petiole terete, 1-2 cm long, glabrous, the pulvinus thick and striate, 0.5-1.0 cm long; stipules elliptic, up to 14 mm long and 2 mm wide, tomentose to glabrous, striate. *Inflorescences* axillary, 1-4 spikes in the defoliated axils or in short, stipulate branchlets; peduncle slender, 1.0-2.5 cm long, glabrous to puberulent; rhachis angulate, 1-2 cm long, the bracts spatulate, reflexed, about 1 mm long. *Flowers* sessile, congested; calyx campanulate, sparsely pilose, 1 mm long, the teeth small and irregular; corolla tubular-funnelform, 4-5 mm long, glabrous or puberulent at the tip, the lobes acute, 1 mm long; staminal tube slightly exserted; ovary oblong, compressed. *Legume* flat, oblong, straight, about 22 cm long, 2 cm wide.

Costa Rica, Panama. (Colombia.) Apparently a rare species, occurring at very different elevations.

COSTA RICA: PUNTARENAS: Río Esquinas, Kil. 42, *Allen 5433* (F, MO).
PANAMA: DARIEN: Yaviza, *Allen 4585* (F, MO).

The present interpretation of this species is based on the study of a photograph of the type and the detailed description of Kunth in H.B.K. (Nov. Gen. Sp. Pl. **6:** 284, 1823). Four collections from Colombia have been examined that match very well the photo and description; the same is true of the Panamanian specimen. It is quite probable that *I. lopadenia* Harms may belong here, as well as some Venezuelan specimens, thus giving more amplitude to the present geographic area.

5. INGA BELICENSIS Standley, Publ. Field Mus. Nat. Hist., Bot. Ser., **4:** 307, 1940. (Type *Schipp 24*)

Trees up to 17 m tall; branchlets terete, puberulent when young, in age glabrate. *Leaves* with 3 pairs of leaflets; leaflets coriaceous, obovate to elliptic, the apex acute to acuminate, the acumen curved, sometimes mucronate, 1.5 cm long,

the base cuneate, often oblique, above lustrous, glabrous, the nerves scarcely prominent, beneath dull, glabrous, the nerves conspicuous, the upper pair obovate to obovate-elliptic, 8-12 cm long, 2.5-4.5 cm wide, the lower pair elliptic and oblique, the basal pair 4-6 cm long, 1.5-2.5 cm wide, petiolules short, 1-2 mm long, pilose; rhachis narrowly winged to marginate, 3-7 cm long, glabrous, the glands stipitate, glabrous, pertuse; petiole terete, 0.5-1.0 cm long, glabrous, the pulvinus thick, one fourth the length of the petiole. *Inflorescences* 1-2 in each axil; peduncle terete, 1.5-3.5 cm long, puberulent, 3 times longer than the rhachis; rhachis 0.5-1.5 cm long, the bracts triangular, less than 1 mm long, pubescent, apparently persistent. *Flowers* sessile, in congested spikes; calyx campanulate, 1.5 mm long, glabrescent, the lobes acute, about 1.5 mm long, pilose; staminal tube exserted. *Legume* flat, oblong, 10-14 cm long, 2.0-2.5 cm wide, glabrous or pilose at the margins, the borders elevated.

Lowlands of British Honduras and adjacent Guatemala.

BRITISH HONDURAS: Baboon Ridge, Stann Creek District, *Gentle 3134* (NY); Mullins River Road, *Schipp 24* (F, MO); Saint Augustin, El Cayo District, *Lundell 6599* (F, GH, NY); Valentin, El Cayo, *Lundell 6325* (F).

GUATEMALA: IZABAL: Bananera to La Presa, *Steyermark 38158* (F).

Inga belicensis is a close ally of *I. fagifolia.* The latter is generally restricted in Central America to the Pacific slope, and it is very possible that the Belice plant represents a variant due to a long isolation. In foliage and fruit the two species practically are indistinguishable, but some minor variations in the shape of the leaflets do occur: for instance, the marked acumination in *I. belicensis.* There is also a trend in this species to have a wider rhachis. The most important differences are in the inflorescence: in *I. fagifolia* the peduncular part is always a fraction of the total axis, while in *I. belicensis* the floral rhachis is restricted to one third the length of the peduncle. The Guatemalan plant is referred here tentatively as it is a sterile specimen.

6. INGA PEZIZIFERA Benth. in Hook., Lond. Jour. Bot. **4:** 587, 1845. (Type *Schomburgk 124* photo)

Feuilleea pezizifera (Benth.) O. Ktze., Rev. Gen. Pl. **1:** 188, 1891.
Inga microstachya Britton & Killip, Ann. N. Y. Acad. Sci. **35:** 115, 1936. (Type *Mutis 3633*)

Trees; branchlets terete, glabrous, markedly pedicellate. *Leaves* with 3-5 pairs of leaflets; leaflets chartaceous, elliptic to lanceolate-elliptic, the apex markedly acuminate, the broad acumen up to 1 cm long, the base rounded to acute, strongly asymmetric, above lustrous, glabrous, the nerves prominent, the upper pair lanceolate-elliptic, 12-18 cm long, 4-7 cm wide, the lower pair lanceolate 7-9 cm long, 3-4 cm wide; the petiolules short, 2 mm long, glabrous; rhachis terete to angulate, generally broader and flattened in the upper part of each interfoliolar section, 7-15 cm long glabrous or puberulent, the glands prominent, crateriform, 2 mm in diam, glabrous; petiole terete, broad at the pulvinar section 1.5-2.0 cm long, glabrous or puberulent; stipules oval-lanceolate, 5-6 mm long, pilose, cadu-

cous. *Inflorescences* spicate, axillary, 1-5 per axil, frequently on defoliated branchlets of the previous growth; peduncle slender, 2.5-4.0 cm long, puberulent; rhachis 1.5-3.5 cm long, the bracts minute, spatulate, about 1.5 mm long; puberulent, semi-persistent. *Flowers* congested, sessile; calyx conic, 1.5-2.0 mm long; corolla tubular-funnelform, 5-6 mm long, sparsely puberulent, the lobes acute, about 1 mm long; staminal tube slightly exserted; ovary oblong, short, sparsely pilose. *Legume* unknown.

Panama. (Colombia to Brazil.)

PANAMA: CANAL ZONE: Barro Colorado Island, *Kenoyer* 363 (US), *Zetek* 3867 (F, MO); Chagres batteries to Fort San Lorenzo, *Maxon & Valentine* 6979 (GH, US).

A species well marked for its fascicled inflorescences, of which there are up to five in each axil, and for its acute to narrowly acuminate leaflets. In many of its foliar characters it remotely resembles *I. ruiziana,* with which it is often confused in the herbaria; the shape of the leaflets, however, is very different in the two species. Some Brazilian specimens, such as *Ducke* 35538, labeled as *I. subsericantha* Ducke, also belong here.

SECTION II. INGA

§ *Evinga* Benth. in Hook., Lond. Jour. Bot. **4**: 606, 1845.
§ *Pseudinga* Benth., loc. cit. 590.

Trees; branchlets terete to angulate, glabrous to densely pubescent. *Leaves* large, with 2 to many pairs of leaflets; leaflets sparsely to densely pilose, the lateral nerves numerous; rhachis winged or terete. *Inflorescence* spicate or racemose, one to several, fascicled in the axils, or paniculate or corymbose at the ends of the branchlets; peduncle generally longer than the rhachis. *Flowers* congested at the tip of the inflorescence, sessile or pedicellate; calyx tubular to turbinate, pubescent in the Central American and West Indian species, sometimes glabrescent; corolla tubular, appressed-pilose. *Legume* flat, tetragonal or subterete, pubescent or glabrate in age. SERIES . . . 1-13

Series 1. **PUNCTATAE** J. León, ser. nov.

Arbor; ramuli teretes vel angulati lenticellati. *Folia* foliolorum paribus 2-4; rhachis teres glandulis sessilibus patelliformibus. *Inflorescentiae* axillares vel brevipedunculatae, 1-multi. *Flores* sessiles vel brevipedicellati; calyx brevis, tubularis, pilosus vel glaber; corolla tubularis, sparse pilosa. *Legumina* plana marginibus elevatis.

Trees; branchlets terete or angulate, pilose to glabrous, lenticellate. *Leaves* with 2-4 pairs of leaflets, glabrous or ferrugineous pilose; rhachis terete, the glands sessile, patelliform. *Inflorescences* axillary or in short spur, 1-many. *Flowers* sessile to shortly pedicellate; calyx short, tubular, pilose or glabrous; corolla tubular, sparsely pilose. *Legume* flat, large or small, the margins elevated.

Type species: *I. punctata* Willd.

This series forms a transition between § *Bourgonia* and the rest of § *Inga*. It is formed by one species of wide distribution and by endemics, some of them poorly known, narrowly distributed species. Four of them occur in Central America and two in the Lesser Antilles. The most aberrant of all is *I. pinetorum* of the pine dunes in the Gulf of Mexico. SPECIES . . . 7-13

a. Branchlets, leaves and legume sparsely pilose to glabrous; calyx regular.
  b. Flowers sessile.
    c. Leaflets flat, elliptic; inflorescences 1-7 per axil; peduncle slender.
      d. Legume 6-16 cm long, 2-3 cm wide.
        e. Calyx pubescent, 3-5 mm long. Mexico to Panama ....7. I. PUNCTATA
        ee. Calyx glabrous, 6-7 mm long. Honduras ....8. I. YUNCKERI
      dd. Legume 20-32 cm long, 3.5-4.0 cm wide, Costa Rica ....9. I. LATIPES
    cc. Leaflets bullate, broadly elliptic; inflorescences solitary, the peduncle stout. Martinique ....10. I. MARTINICENSIS
  b. Flowers pedicellate.
    f. Upper leaflets 11-18 cm long. Mexico ....11. I. BREVIPEDICELLATA
    ff. Upper leaflets 8-10 cm long. Dominica ....12. I. DOMINICENSIS
aa. Branchlets, leaves and legume densely pilose; calyx often cleft. Mexico, British Honduras ....13. I. PINETORUM

7. INGA PUNCTATA Willd. in L., Sp. Pl. **4:** 1016, 1810. (Type *Hoffmannsegg s.n.* photo)

Mimosa sericea Poir. in Lam., Encycl. Suppl. **1:** 42, 1810 (pro parte). (Based partially on *Inga punctata* Willd.)
Inga leptoloba Schlecht., Linnaea **12:** 560, 1838. (Type *Schiede s.n.*)
I. punctata Willd. var. *panamensis* Benth., Trans. Linn. Soc. **30:** 613, 1875. (Type *Fendler 89*)
Feuilleea leptoloba (Schlecht.) O. Ktze., Rev. Gen. Pl. **1:** 188, 1891.
F. punctata (Willd.) O. Ktze., loc. cit.
Inga popayanensis Pittier, Contr. U. S. Nat. Herb. **18:** 185, 1916. (Type *Lehmann 5751*)
I. ierensis Britton, Bull. Torrey Bot. Club **50:** 52, 1923. (Type *Britton & Hazen 1627*)
I. punctata Willd. subsp. *chagrensis* Pittier, Jour. Dept. Agr. Porto Rico **13:** 135, 1929. (Type *Maxon 4788*)

Trees 6 to 15 m tall; branchlets terete or angulate, strigose-puberulent when young, glabrate in age, densely lenticellate. *Leaves* with 2-3 pairs of leaflets; leaflets elliptic to lanceolate, the apex obtuse, acute or acuminate, mucronate, the base rounded to cuneate, above lustrous, strigose-pubescent, the lateral nerves slightly prominent, straight, parallel, with the reticulate nervation conspicuous on both sides, beneath paler, sparsely pilose except on the costa and main nerves which are densely pubescent and markedly prominent, the upper pair elliptic-lanceolate, 6-17 cm long, 3-7 cm wide, the basal pair lanceolate to ovate, 3-11 cm long, 1-5 cm wide, the petiolules 1-4 mm long, pubescent; rhachis terete or submarginate, 2-11 cm long, shortly pilose to glabrate, the glands orbicular to patelliform, often obsolete; petiole terete, 1-3 cm long appressed-pubescent to glabrate, the pulvinus darker and thicker, about 1 cm long; stipules subulate, 3-8 mm long, pilose, caducous. *Inflorescences* solitary or in groups of 2-7, fascicled at the axils, or paniculate on spurs or terminal branchlets; peduncle angulate, 1.5-5.0 cm long, appressed-pilose; rhachis 0.5-3.0 cm long, densely pilose, the bracts lanceolate, acute, 2-3 mm long, pubescent, caducous. *Flowers* sessile; calyx subturbinate 3-5 mm

long, puberulent, the teeth irregular, about 0.5 mm long; corolla tubular, expanded above, 4-10 mm long, appressed-pilose, the lobes lanceolate, 1-2 mm long; staminal tube included to slightly exserted, the free part of the filaments about 1 cm long; ovary and style glabrous, the stigma capitate. *Legume* flat, straight to arcuate, oblong, 4-16 cm long, 2-3 cm wide, mucronate at the apex, rounded at the base, sparsely pilose when young, in age glabrate, the borders prominent; seeds 4-20, oblong, thick, 1-2 cm long, the aril fleshy.

Mexico to Panama; Trinidad and Tobago. (Northern part of South America.)

Vernacular names: *acotope* (Veracruz-Ll. Williams); *paterno, cerel, ixcapirol, pepeto* (Guatemala-Standley); *pepeto negro* (El Salvador-Standley); *cuajiniquil* (Costa Rica).

MEXICO: CHIAPAS: Escuintla, Monte Ovando, *Matuda 16046* (EAP, F); La Suiza, *Matuda 1915* (EAP, F, K, NY, US). OAXACA: Choapam, Yaveo, *Mexia 9258* (F, GH, MO, NY); Concordia, *Morton & Makrinius 2489* (F, US), *Reko 3618* (US); Tuxtepec, *Nelson 377* (NY). TABASCO: Balancan, Reforma, *Matuda 3220* (F, NY); San Juan Bautista-Atasta, *Rovirosa 128* (US); Tenosique, Boca Cerro, *Matuda 3548* (F, MO, NY). VERACRUZ: Barranca de Panoya, *C. A. Purpus 8556* (GH, MO, US); Cabrestos, *Liebmann 4428* (F, US); Córdoba, *Bourgeau 2043* (GH, K), *2320* (GH, US); Fortin *C. A. Purpus 8599* (GH, MO, NY, US); Fortuño, *Ll. Williams 8991* (F); Hacienda de Jovo, *Liebmann 4434* (F, US); Jalapa, Hacienda La Laguna, *Schiede s. n.* (F, GH, MO); Mata de San Juan, *Liebmann 4435* (F, US); Mirador, *Liebmann 4436* (F. GH, US), *Seler 5139* (GH), *5142* (GH); Potrero de Cazadero, *Liebmann 4433* (F); Santa Lucrecia, *Mell 520* (F, NY, US), *577* (F, US), *C. L. Smith 1146* (EAP, GH, MO, NY); Tantoyuca, *Ervendberg 4* (GH); Tezonapa, *Orcutt 3113* (F); Zacualpán *C. A. Purpus 8165* (F, GH, MO, NY, US), *8168* (GH, MO, NY, US), *8584* (GH, MO, NY, US), *10696* (GH, NY, US), *10719* (NY, US), *10784* (NY, US), *11696* (GH, NY, US), *10719* (NY, US), *10784* (NY, US), *11696* (NY, *14001* (F, MO, NY). WITHOUT LOCALITY: *Kerber 403* (US), *Sessé, Mociño, etc. 3773* (F), *3785b* (F).

BRITISH HONDURAS: BELIZE: Belize River, *Cook & Martin 34* (US); Manatee Lagoon, *Peck 334* (GH); Sibun River, *Bartlett 11369* (GH, NY, US), *Gentle 1520* (F, MO, NY, US), *1723* (F). EL CAYO: Cocquericot, *Bartlett 12068* (F, NY, US); Vaca, *Gentle 2451* (F, MO). STANN CREEK: Big Creek, *Schipp 163* (F, GH, NY, US); El Dorado, *Schipp 403* (F); Middlessex, *Schipp 380* (F, GH, K, MO, NY), *Gentle 2729* (F, NY, US); Mullins River, *Schipp 23* (F, GH, MO, US). WITHOUT LOCALITY: *Peck 571* (GH).

GUATEMALA: ALTA VERAPAZ: Gubilgüitz, *Steyermark 44333* (F), *Tuerckheim 8195* (GH, NY, US); Sepacuité, *Cook & Griggs 491* (US), *636* (US), *Owen 2* (US); Setzimaj, *Cook & Griggs 51* (US), *52* (US), *53* (US); Tactic, *Standley 90400* (F). CHIMALTENANGO: Panajabal, *Standley 62134* (F). ESCUINTLA: Las Lajas, *Standley 64821* (F); Pacayal, Sta. Emilia, *Bequaert 29* (F, GH). IZABAL: Los Amates, *Kellermann 7147* (NY); Morales, *Kellermann 6109* (US); Quiriguá, *Standley 24487* (GH, NY, US); Río Chacón, *H. Johnson 1201* (US); Sta. Inés, *Galusser 7* (F). PETEN: La Libertad, *Aguilar 419* (F, NY), *Lundell 2105* (US), *3090* (US). QUEZALTENANGO: Colombia, *Skutch 1332* (F); San Francisco de Miramar, *Pittier 68* (NY, US); Sta. María de Jesús, *Standley 68404* (F). SANTA ROSA: Las Viñas, *Heyde & Lux 6094* (F, GH, MO, NY, US). SUCHITEPEQUEZ: San Augustín, *Steyermark 48068* (F); Volcán Zunil, Monte Cristo, *Steyermark 35222* (F). WITHOUT LOCALITY: *Record & Kuylen 72* (GH, NY, US).

EL SALVADOR: AHUACHAPAN: Ataco, *Standley & Padilla 2710* (F). CABANAS: San Nicholás, *Calderón 1574*, (GH, MO, NY, US). LA LIBERTAD: Comasagua, *Calderón 1354* (GH, MO, NY, US); Santa Tecla, *Levy 784* (EAP). LA UNION: La Unión, *Carlson 663* (F). SANTA ANA: Metapán, *Carlson 785* (F). WITHOUT LOCALITY: *Renson 328* (US), *Calderón 2255* (NY, US).

HONDURAS: ATLANTIDA: Tela, *Standley 54532* (F, US), *56616* (F, US), *56870* (F, NY, US). COMAYAGUA: Pito Solo, *Edwards 436* (F), *467* (F, US). CORTES: Río Lindo, *Williams & Molina 17635* (EAP); San Pedro Sula, *Thieme 5209* (GH, US). OLANCHO: Catamarcas,

Standley 18233 (F). TEGUCIGALPA: Mata de la Flor, *von Hagen 1140* (F, NY). YORO: Subirana, *von Hagen 1099* (F, NY).

NICARAGUA: ZELAYA: Braggman's Bluff, *Englesing 238* (F); Toumarin, Río Grande, *Molina 2414* (EAP).

COSTA RICA: ALAJUELA: La Calera, San Ramón, *Brenes 11575* (CR, F); La Palma, San Ramón, *Brenes 5353* (CR, F); Piedades, San Ramón, *Brenes 5478* (CR, F); San Carlos, *Cook & Doyle 92* (US), *Pittier 16698* (NY); San Luís de Zarcero, *A. Smith 1366* (F, NY); San Pedro, San Ramón, *Brenes 4442* (CR, F), *4677* (CR, F), *5093* (F), *6632* (CR, F); San Miguel, San Ramón, *Brenes 17040* (CR, F); Villa Quesada, *A. Smith 2929* (MO). CARTAGO: Cartago, *Stork 1223* (F); Dulce Nombre, *Standley 35882* (US); La Carpintera, *Standley 34508* (US); Turrialba, *Holdridge 2570* (IAIAS), *2571* (IAIAS), *León 1522* (IAIAS), *3811* (IAIAS), *3814* (IAIAS), *3821* (IAIAS). GUANACASTE: Líbano, *Standley & Valerio 44919* (F, NY, US); Santa Maria, *Dodge & Thomas 6262* (F, GH, MO, NY); Tilarán, *Standley & Valerio 44171* (F, NY, US), *44507* (F, NY, US), *44508* (F, NY, US), *46086* (F, NY, US). HEREDIA: Barba, *León 400* (CR, F); Río Ciruelas, *Biolley 3230* (US); San Francisco, León *3830* (IAIAS): Sto. Domingo, *Echeverría 314* (CR, F), *315* (CR, F). LIMON: Limón, *Standley 27270* (US); Shirores, *Tonduz 9354* (CR, F), *9355* (CR, F). PUNTARENAS: Golfito, *Allen 5620* (EAP, F); Puerto Jiménez, *Brenes 12223* (CR, F); Río Sándalo, *Dodge & Georger 10431* (F, MO). SAN JOSE: Cuesta de Tarrazú, *Tonduz 7859* (US); El General, *Skutch 3915* (MO, NY); San José, *Holway s. n.* (US), *Inst. Phys. Geogr. Costa Rica 17146* (US), *Jiménez 821* (US), *Standley 33286* (US), *34786* (US), *41207* (NY, US), *Tonduz 7020* (CR, MO, NY, US); Santa María de Dota, *Standley 42451* (NY, US), *42522* (NY, US).

PANAMA: BOCAS DEL TORO: Bocas del Toro. *Carleton 176* (GH); Changuinola Valley, *Cooper & Slater 73* (F, NY), *100* (US), *Dunlap 551* (F); Chíriquí Lagoon, *von Wedel 1069* (GH, MO), *1230* (GH, MO); Fish Creek, *von Wedel 2357* (MO), *2387* (GH, MO, NY). CANAL ZONE: Barro Colorado Island, *Avilés 116* (F), *Bailey 620* (F), *764* (F), *Bangham 461* (F), *Kenoyer 366* (US), *Shattuck 339* (F), *751* (F), *Wetmore & Abbe 181* (F, GH), *Woodworth & Vestal 359* (F), *Zetek 3468* (F), *3485* (F), *3837* (F, MO), *3847* (F, MO), *3848* (F), *3849* (F); Chagres, *Fendler 89* (GH, MO); Culebra, *Pittier 2309* (NY, US); Fort Sherman, *Standley 30950* (US), *31162* (US); Gatún, *Hayes 55* (NY), *Goldman 1865* (US), *Maxon 4788* (GH, MO, NY); Río Chagres, *Steyermark & Allen 16778* (GH); Vigía, *Dodge, Steyermark & Allen 16530* (GH, MO). CHIRIQUI: Boquete, *Davidson 473* (F), *814* (F), *Little 6053* (MO). COCLE: Valle de Antón, *Allen 2773* (US), *3700* (F, MO). COLON: Río Culebra, *Pittier 4161* (NY, US). DARIEN: El Real, *Allen 966* (GH, MO, NY); Pinogana, *Allen 4281* (MO). PANAMA: Chepo, *Hunter & Allen 95* (F, GH, MO, US), *Klug 33* (US); Río Tapia, *Standley 28084* (NY, US). VERAGUAS: Tabasara to Sona, *Woodson, Seibert & Allen 489* (MO). PROVINCE UNKNOWN: Bayares River, *Mell s. n.* (NY). WITHOUT LOCALITY: *Seemann 406* (GH).

TRINIDAD: without locality, *Britton & Hazen 1627* (US).

TOBAGO: Crown Grace, *Broadway 3909* (F, MO); The Widow. *Broadway 4652* (F, MO, NY).

In Mexico and Central America this species has been divided into *I. punctata* and *I. leptoloba* on the basis of the number of pairs of leaflets, two in the first, three in the second. Another differential character, mentioned by Pittier, is the shape of the base of the leaflet, rounded and wide in *I. punctata,* cuneate in *I. leptoloba.* More recently, however, the trend is to consider these species as forming a single one (cf. Schery, Ann. Missouri Bot. Gard. **37:** 221, 1950), since the variability shown by the specimens points to no consistent difference that would justify a specific segregation. After considerable study of the specimens mentioned the conclusion here reached agrees with the reduction of *I. leptoloba.* It seems necessary, however, to observe that there are some interesting points to consider for future studies: 1) In Mexico, British Honduras and Guatemala no specimen has only bijugate leaves, while the collections with trijugate leaves only form a very high percentage, and the mixed (some leaves with two pairs, others

with three in the same collection) are very rare. In contrast, 88% of the specimens from Panama have bijugate leaves, while in the intervening countries the number of collections with two and three pairs are more or less equal; 2) Measurements of the basal angle of the leaflet show that the modal value in *I. leptoloba* is smaller than in *I. punctata,* but that the total ranges overlap and no clear trend is observable; 3) There is a group of specimens from the Atlantic lowlands of Nicaragua to Panama that have large legumes, comparable in size to those of *I. latipes*—possible relationship based on this and other characters between these two species remains obscure; 4) There are some local variants, such as the trees with small, very lustrous leaflets from Costa Rica (for instance, *Dodge & Thomas 6262*), or the Panamanian "subspecies" described by Bentham and by Pittier; 5) *Inga yunckeri* of the Atlantic coast of Honduras seems to be very close to *I. punctata,* but at present no intergrading material is available; 6) Finally, the specimens from Mexico, including the type of *I. leptoloba,* seem to be the extreme in a line of variation and offer some marked characteristics, while at the other extreme of the geographic range (northern South America) the variability is more complicated, especially when some other doubtful species, such as *I. strigillosa* Benth., have to be considered. In this case it seems that although the herbarium methods show the convenience of reducing the different populations under one species, they also point the necessity of field studies, which eventually may change the position accepted here.

8. INGA YUNCKERI Standley, Publ. Field Mus. Nat. Hist., Bot. Ser., **9:** 296, 1940. (Type *Yunker, Koepper & Wagner 8805*)

Trees about 9 m tall; branchlets terete, striate, glabrous, lenticellate. *Leaves* with 2 pairs of leaflets; leaflets elliptic to ovate, the apex acute to acuminate, the base oblique, cuneate, above lustrous, glabrous, the nerves slightly prominent, beneath lustrous and glabrous, the lateral nerves and costa very prominent, the reticulate nervation conspicuous, the upper pair elliptic, 16-20 cm long, 6-10 cm wide, the basal pair ovate, about 9 cm long, 5 cm wide; rhachis terete, 2.5-7.5 cm long, glabrous, the glands small, cupuliform; petiole terete, 1.5-20 cm long, glabrous, the pulvinus thicker and darker. *Inflorescences* numerous, in short terminal branchlets; peduncle slender, 1.0-2.5 cm long, puberulous; rhachis 1-2 cm long, pubescent, the bracts minute, caducous. *Flowers* sessile, congested; calyx tubular, 6-7 mm long, glabrous, striate, the teeth very short and obtuse; corolla tubular, spreading above, 10-12 mm long, densely sericeous, the lobes acute, about 1 mm long; staminal tube included, the free part of the filaments about 2 cm long. *Legume* unknown.

Atlantic lowlands of Honduras.

HONDURAS: ATLANTIDA: vic of La Ceiba, *Yuncker et al. 8805* (F, MO).

This poorly known species is closely related to *I. punctata* from which it differs in the larger flowers and glabrous calyx and leaves. It is here maintained as a separate species owing to the lack of intergrading specimens, but it seems to be only an aberrant form of *I. punctata.*

9. Inga latipes Pittier, Contr. U. S. Nat. Herb. **18:** 183, 1916. (Type *Tonduz 13056*)

Trees; branchlets angulate, glabrous. *Leaves* with 3 pairs of leaflets; leaflets ovate to elliptic, coriaceous, the apex obtuse to acuminate, the base cuneate to rounded, above lustrous, glabrous, the nerves slightly prominent, beneath paler, glabrous, the nerves very prominent, the upper pair elliptic, 8-11 cm long, 3-5 cm wide, the basal pair lanceolate to ovate, 3-4 cm long, 1.5-2.0 cm wide, the petiolule 2 mm long, sparsely pilose; rhachis terete or canaliculate above, 3-4 cm long, glabrous, the glands prominent, hemispheric, with a narrow apical pore; petiole terete, 1.0-1.5 cm long, glabrous, the pulvinus thick and darker. *Inflorescences* axillary, solitary; peduncle terete, about 1.5 cm long, glabrous; rhachis 2.0-2.5 cm long. *Flowers* unknown. *Legume* flat, oblong, the irregular shape due mostly to a lack of development of some seeds, 20-32 cm long, about 4 cm wide, blackish, glabrous, transversely striate, the borders elevated.

Costa Rica: cartago: Las Vueltas, Tucurrique, *Tonduz 13056* (GH, NY, US).

This species is known only from fruiting specimens and its position among the gymnopodae where Pittier placed it is open to doubt. The general appearance of the plant recalls some forms of *I. punctata,* but its fruits are larger than any known from that species. However, there are several collections referred to the last species in which the legumes reach a size comparable to those of *I. latipes.* Such collections are: *Standley 19361,* from El Recreo, Dept Zelaya, Nicaragua; *Standley 30720,* from Guápiles, Prov Limón, Costa Rica; *Barbour 1045,* from Siquirres, Prov Limón, Costa Rica and *G. P. Cooper 492,* from Cricamola, Prov Bocas del Tora, Panama. All these collections are in fruit only, and the legumes exhibit a size unusual for *I. punctata* and the indument on the rhachis of leaves and branchlets is also denser than in the common forms of *I. punctata.* Only more complete material will clarify the problematic position of these collections and the relation, if any, between *I. latipes* and *I. punctata.* Although *I. latipes* was published by Pittier in 1916, it is interesting to note that he does not mention the species in his treatment of the Central American species of *Inga* published in 1929.

10. Inga martinicensis Presl, Symb. Bot. **1:** 65, 1832. (Type *Kohaut s.n.,* Sieber distr. 325)

Mimosa fagifolia Jacq., Select. Stirp. Amer. Hist. 264, 1763, non L. (ex char.)
M. sericea Poir. in Lam., Encycl. Suppl. **1:** 42, 1810 (pro parte).

Trees, the trunk and branches frequently crooked; branchlets terete, ferrugineous-tomentose to glabrescent, lenticellate. *Leaves* large, with 1-3 (generally 2) pairs of leaflets; leaflets coriaceous, elliptic, bullate, the apex acute, rounded or emarginate, the base acute to rounded, often asymmetric, above lustrous, pilose when young, in age glabrate, the 6-9 main nerves deeply impressed, giving a typical bullate appearance to the blade, beneath glabrous or sparsely pilose, mainly along the prominent nerves, the upper pair broadly elliptic, 9-16 cm long, 5-11 cm

wide, the basal pair elliptic to ovate-elliptic, 5-12 cm long, 5-7 cm wide; rhachis terete or marginate, 3-7 cm long, tomentose or glabrous, the glands small, cupuliform, pertuse; petiole terete to angulate, 1.5-3.5 cm long, tomentose to glabrescent, the pulvinus terete and short; stipules ovate, acute, 1-3 mm long, glabrous or tomentose, caducous. *Inflorescences* axillary, solitary; peduncle terete, 1.5-2.0 cm long, pubescent; rhachis 3-6 cm long, tomentose the bracts linear, 1.5 mm long, tomentose, caducous. *Flowers* sessile, congested; calyx campanulate 3.5-5.0 mm long, sericeous, the teeth irregular sometimes up to 2 mm long, often shorter, corolla funnelform, 7.0-8.5 mm long, sericeous, the lobes acute 2 mm long; staminal tube included, the free part of the filaments about 12 mm long; ovary pubescent. *Legume* flat, oblong, straight or slightly curved, mucronate, 10-15 cm long, 2.0-2.5 cm wide, about 0.5 cm thick, densely ferrugineous-pubescent when young, in age glabrate, the borders elevated.

Highland forests and savannas of Martinique and Guadaloupe.

Vernacular name: *pois-doux montagne* (Martinique—Duss).

GUADELOUPE: savanes aux Ananas, morne du Motelayne, *Duss 3230* (NY, US).

MARTINIQUE: Citame, *Stehlé 1391* (NY); Pitons de Carbet, *Duss 1155* (NY), *Stehlé 2177* (NY), *Stehlé 2392* (US); without locality, *Kohaut s. n.*, Sieber distr. 325 (GH, MO).

Presl based his description of *I. martinicensis* on the Kohaut collection that Sieber distributed under the name of *Mimosa coriacea.* It is frequently confused with *I. coruscans* H.B.K., a species of South and Central America, and Grisebach refers to *I. martinicensis* the type collection of *I. dominicensis* Benth., a very distinct species.

The description of *I. fagifolia* Jacq. (non L.) agrees in general with the characters of *I. martinicensis,* and the crude illustration in Stirp. Amer. Hist. *t. 164* undoubtedly represents this species. The plate shows, for instance, a leaf with only one pair of leaflets, a striking character that occurs sometimes in *I. martinicensis.* Poiret based his description of *Mimosa sericea* partially on Jacquin, and took the rest from the original description of *I. punctata* Willd.

Inga martinicensis seems to be related to *I. punctata,* a species that occurs in the West Indies only in Trinidad and Tobago.

11. INGA BREVIPEDICELLATA Harms in Fedde, Rep. Sp. Nov. **19:** 62, 1924, (ex char.; Type *J. A. Purpus 282*, not seen)

Trees; branchlets terete, glabrous, sparsely lenticellate, in age whitish and with a soft bark. *Leaves* with 3 pairs of leaflets; leaflets shortly petiolulate, oblong to oblong-obovate, the apex acute to long acuminate, the acumen up to 2 cm long, ending in a short and strong mucro, the base generally acute, rarely obtuse, above dark green, lustrous and glabrous, the nerves impressed, beneath sparsely pilose to glabrous, the 12-14 pairs of lateral nerves prominent with alternate and shorter ones between, the upper pair oblong, 11-18 cm long, 5-7 cm wide, the lower pairs oblong to oblong-obovate, the lowermost 6-9 cm long, 3-4 cm wide; the petiolules 2-4 mm long; rhachis narrowly marginate, 1.5-6.5 cm long, glabrous, the glands small, disciform, sometimes obsolete; petiole terete, 2.5-3.5 cm long,

striate, the pulvinar section conic and darker; stipules oblanceolate, 9-11 mm long, striate, pubescent, caducous. *Inflorescences* solitary or in groups of 2-3, fascicled below the new growth; peduncle slender, 4-7 cm long, striate, pilose; rhachis 1.5-2.5 cm long. *Flowers* dense, the lower with thin, pilosulose pedicels up to 2 mm long, the upper almost sessile; calyx tubular-funnelform, 2.5-3.0 mm long, sparsely pilose, more densely pilose at the base and tips, the teeth obtuse about 1.5 mm long; corolla tubular-funnelform, 6 mm long, appressed-pilose, the lobes 1.0-1.5 mm long; staminal tube included, the filaments up to 1.5 cm long. *Legume* flat, oblong, 18-22 cm long, 4-5 cm wide, less than 1 cm thick, transversely striate when young, glabrous, the borders elevated.

Highlands of Veracruz.

Mexico: veracruz: Mirador, *C. A. Purpus 10702* (NY, US), *10884* (US), *16007* (US); Zacualpán, *C. A. Purpus 8169* (GH, MO, NY, US), *8394* (GH, MO, NY, US), *8400* (GH, MO, NY, US), *10106* (F).

The species is noteworthy for its shortly pedicellate flowers and large fruits. In some characters there is a striking similarity between this species and *I. jinicuil*, especially in the shape and size of the leaflets and fruits, in the oblanceolate stipules and the structure of the bark in the oldest branchlets. In fact, the specimens in fruit are very difficult to differentiate. Their area of distribution is also more or less the same. In the general appearance of the inflorescences *I. brevipedicellata* looks like *I. punctata*, with which it is often confused in herbaria.

As far as known this species is restricted to one highland of Veracruz, where it is commonly planted as a shade tree in the coffee fields. The type from Mirador, was not available, and comes from a cultivated tree.

12. Inga dominicensis Benth., Trans. Linn. Soc. **30:** 612, 1875. (Type *Imray* 336)

Trees, branchlets terete or angulate, puberulous to glabrous, markedly lenticellate. *Leaves* small with 2-3 pairs of leaflets; leaflets coriaceous, ovate-lanceolate to elliptic, the apex acute, the base acute to rounded, above lustrous, glabrous, the distant nerves slightly prominent, beneath dull, sparsely pilose when young, in age glabrate, the nerves prominent, the upper pair ovate-lanceolate, 8-10 cm long, 2.5-5.0 cm wide, the basal pair elliptic, 4-6 cm long, 2-3 cm wide; rhachis slightly marginate, 1-2 cm long, glabrous, the glands minute, cupuliform, pertuse; petiole terete, the pulvinar section thicker, 1.0-1.5 cm long. *Inflorescences* solitary and axillary; peduncle slender, puberulous, about 1 cm long; rhachis angulate, 2-3 cm long, puberulous, the bracts triangular, less than 0.5 mm long. *Flowers* shortly pedicellate; calyx campanulate, about 3 mm long, strigillose, the teeth obtuse and inconspicuous; corolla funnelform, about 5 mm long, pilose, the lobes acute, 1.5-2.0 mm long; staminal tube included. *Legume* unknown.

Highland forests of Dominica.

Dominica: without locality, *Imray* 336 (GH, K).

Bentham separated the Imray collection from *I. martinicensis*, where Grisebach (Fl. Br. W. Ind. 227, 1861) had put it, on the basis of foliar and floral characters:

the leaflets in *I. dominicensis* have narrow, acuminate apices while in *I. martinicensis* they are obtuse to rounded; the flowers in the first species are shortly pedicellate, in the second sessile or almost so. These two species seem to come from a common stock of South American origin, but probably have undergone a long isolation, not only from each other but also from the species of the mainland, since the area from Guadeloupe to Martinique is geologically the oldest in the Lesser Antilles.

13. INGA PINETORUM Pittier, Contr. U. S. Nat. Herb. **18:** 185, 1916. (Type *Peck 343*)

Small *trees*; branchlets terete, lenticellate, densely ferrugineous-hispid to glabrescent. *Leaves* with 2, rarely 3, pairs of leaflets; leaflets elliptic to obovate, often oblique, the apex rounded, acute or shortly acuminate, the base cuneate and frequently asymmetric, above dark, lustrous, pilose especially along the nerves and margin, or glabrescent, beneath more densely ferrugineous-pilose, the nerves prominent and more pubescent, the upper pair obovate, 6-15 cm long, 3-7 cm wide, the basal pair elliptic to rhombic, 4-10 cm long, 2-4 cm wide, the petiolules terete, pilose, 2-3 mm long; rhachis terete, 2-4 cm long, hispidulous, the glands stipitate, urceolate, 1 mm in diam, glabrous; petiole terete, 1.0-2.5 cm long, densely ferrugineous-hispidulous, stipules triangular, 3-4 mm long, about 2 mm wide, glabrescent, persistent. *Inflorescences* axillary, solitary or in groups of 2-3; peduncle slender, 2.5-7.0 cm long, densely ferrugineous-pilose; rhachis 1-2 cm long, pilose, the bracts triangular, 1.5 mm long, pubescent, caducous. *Flowers* sessile to shortly stipitate; calyx tubular, sometimes deeply cleft on one side, 5 mm long, hispidulous to glabrescent, the teeth acute, 0.5-1.5 mm long; corolla tubular, spreading above, 10-11 mm long, densely hispid, the lobes acute, 1-3 mm long; staminal tube exserted. *Legume* (immature) flat, oblong, up to 7 cm long, 2.5 cm wide, densely fulvous-hispidulous when young, in age glabrate.

Lowlands of Mexico and British Honduras in dry forests; frequent in the pine formations close to the sea.

Vernacular name: *tama-tama* (British Honduras).

MEXICO: TABASCO: Achotal, Balancán, *Matuda 3098* (F, NY); Chiltepec, *Rovirosa 738* (K, US). VERACRUZ: Coatzacoalcos, *C. L. Smith 986* (EAP, US).

BRITISH HONDURAS: All Pines, *Schipp 767* (F, GH, MO, NY); Manatee Lagoon, *Peck 343* (GH); Monkey River, *Gentle 4149* (MO, NY, US); Mountain Pine Ridge, *Bartlett 13086* (NY, US), *Lundell 6747* (F, GH, NY, US).

This species differs from others in the series PUNCTATAE in its dense and ferrugineous pubescence found upon all parts of the plant. It is closely related to *I. punctata,* although it is easily separated from this species by the longer flowers and the type of pubescence. *Inga pinetorum* is found often on the dunes close to the sea.

Series 2. **MULTIJUGAE** J. León, ser. nov.

Arbor vel frutex; ramuli glabri vel puberuli. *Folia* foliolorum paribus 4-10; rhachis teres glandulis patelliformibus. *Inflorescentiae* in lignum vetum axillares,

in ramis juventibus paniculatae; calyx tubularis; corolla tubularis pilosa. *Legumina* plana marginibus elevatis.

Trees or shrubs; branchlets glabrous or shortly pubescent. *Leaves* with 4-10 pairs of leaflets, very variable in size and shape, glabrous or sparsely pubescent; rhachis terete, the glands patelliform. *Inflorescences* axillary in the old wood or paniculate in the new growth; calyx tubular, short or long, cleft in one species; corolla tubular, pilose. *Legume* flat, less than 20 cm long, the margins elevated.

Type species: *I. multijuga* Benth.

This series is formed, with one exception, of species of wide distribution and variability. SPECIES . . . 14-17

a. Corolla more than 10 mm long; upper leaflets oblong to lanceolate.
  b. Flowers congested; foliar rhachis 9-20 cm long; calyx regular.
    c. Calyx 12-22 mm long; 5-10 pairs of leaflets; leaflets apex obtuse to acuminate .... 14. I. MULTIJUGA
    cc. Calyx 3-4 mm long; 4-7 pairs of leaflets; leaflets acute at the apex .... 15. I. THIBAUDIANA
  bb. Flowers distant; foliar rhachis 4-9 cm long; calyx often cleft on two sides .... 16. I. SKUTCHII
aa. Corolla less than 10 mm long; upper leaflets obovate .... 17. I. RUIZIANA

14. INGA MULTIJUGA Benth., Trans. Linn. Soc. **30:** 615, 1875. (Type *Hayes 645*)

Inga aestuarium Pittier, Contr. U. S. Nat. Herb. **18:** 183, 1916. (Type *Tonduz 6793*)

Small *trees* with low branching; branchlets terete, densely ferrugineous-tomentose when young, in age glabrate and lenticellate. *Leaves* with 5-10 pairs of leaflets; leaflets oblong to lanceolate, generally oblique, the apex rounded or obtuse to acuminate, with a short mucro, the base obtuse to rounded, often asymmetric, above lustrous, sparsely pilose to glabrous, densely pilose along the margins and costa, the nerves slightly impressed, beneath paler, densely ferrugineous-pilose, the nerves prominent, the upper pair lanceolate-elliptic, rarely oblong, 7-14 cm long, 3-5 cm wide, the basal pair lanceolate, 2.5-9.0 cm long, 1.0-4.5 cm wide, the petiolule terete, up to 3 mm long, pubescent; rhachis terete, marginate or slightly winged in the upper interfoliolar sections, 9-20 cm long, densely ferrugineous-tomentose, the glands patelliform, glabrous, the rim elevated and paler than the pore; petiole terete, slightly thicker at the pulvinar section, 1.5-2.5 cm long, densely ferrugineous-tomentose; stipules minute, ovate, about 3 mm long, caducous. *Inflorescences* axillary or terminal, solitary or geminate in the axils, or several in short terminal branchlets; peduncle terete, 1.5-5.5 cm long, densely tomentose; rhachis 1.5-2.0 cm long, the bracts minute, triangular, about 1 mm long, pubescent, caducous. *Flowers* sessile, in rather loose spikes; calyx tubular, 7-10 mm long, striate, densely ferrugineous-tomentose, the teeth less than 1 mm long, acute, regular; corolla tubular, spreading above, 12-22 mm long, sericeous, the lobes about 2.5 mm long; ovary flat, glabrous. *Legume* flat, oblong, straight or curved, 15-19 cm long, 1.5-3.0 cm wide, transversely striate, densely tomentose when young, in age glabrate, the borders elevated.

Lowlands of Costa Rica and Panama; often growing along the coasts and estuaries.

Vernacular name: *guabo de estero* (Costa Rica—Pittier).

COSTA RICA: PUNTARENAS: Boca Zacate, Río Térraba, *Tonduz 6793* (CR, US); Isla del Caño, *Holdridge s. n.* (IAIAS); Playa Blanca, Osa, *M. Valerio 469* (CR, F); Puerto Jiménez, *Brenes 12164a* (F); Río de Jesús María, Esparta, *León 3505* (IAIAS).

PANAMA: CANAL ZONE: Barro Colorado Island, *Bangham 533* (F); Chagres, *Fendler 51* (GH, MO, US); Fort Sherman, *Standley 30958* (US); Gatun Lake, *Nielsen 100* (MO), *101* (MO), *115* (MO), *118* (MO); Lion Hill Station, *Hayes 645* (F, K); Margarita Swamp, *Maxon & Valentine 7058* (US); without locality, *Epplesheimer s. n.* (F). VERAGUAS: Isla de Coiba, *Méndez 146* (US).

Within its restricted geographic area, *I. multijuga* offers a morphological variability such as few species in this genus. In the same tree the new growth produces leaves with 8-10 pairs of narrowly elliptic, thin leaflets, and solitary or geminate inflorescences with long calyces, while in the older branchlets the elliptic-lanceolate, subcoriaceous leaflets are arranged in 7-8 pairs and the inflorescences are numerous, terminal and with short calyces. Great variability is found also in different parts: the calyx length ranges from 4-10 mm long; the rhachis varies from terete to clearly winged; and in the leaflets the variability is reflected both in their number per leaf and in the shape, which varies at the apex from obtuse and mucronate to acute and long-acuminate. Small wonder, then, that Pittier attributed *Fendler 51* at GH *to I. ruiziana* G. Don, while the same number at MO and US was determined as *I. multijuga.* The Nielsen collections permit establishing a neat relation between the two types of growth.

Inga aestuarium Pittier may be included under *I. multijuga* perhaps as a subspecific variant. The plants under that name are small trees, which grow mainly on the borders of the sea and estuaries in the Pacific coast of Costa Rica, with fewer pairs of leaflets than is typical of *I. multijuga.* A specimen from Coiba Island, *Mendez 146,* seems intermediate between the Costa Rican and the other Panamanian specimens.

Inga brunnescens Britton & Killip (Type *Mutis* 3523) of central Colombia is very close to *Fendler 51* (GH) and is probably another variant of *I. multijuga.*

15. INGA THIBAUDIANA DC., Mém. Leg. **12:** 439, 1825. (Type *Thibaud s.n.* photo)

I. gladiata Desv., Ann. Sc. Nat., sèr. 1, **9:** 427, 1826 (*fide* Bentham).
I. tenuiflora Salzm. ex Benth. in Hook., Lond. Jour. Bot. **4:** 596, 1845. (Type *Salzmann s. n.*).
I. macradenia Mart. ex Benth., Trans. Linn. Soc. **30:** 615, 1875 (*fide* Bentham).
I. recordii Britton & Rose ex Standley, Trop. Woods **7:** 5, 1929. (Type *Record 40*).

Medium to large *trees;* branchlets terete, lenticellate, densely ferrugineous-pubescent, striate. *Leaves* with 4-7 (generally 5-6) pairs of leaflets; leaflets very variable in shape and size, strongly asymmetric, elliptic to oblanceolate, the apex acute to long-acuminate, the acumen often asymmetric, the base cuneate or rounded, oblique, above lustrous, sparsely pilose except along the nerves and margins where the pubescence is thicker, the nerves slightly prominent, beneath dull, closely pilose, the nerves prominent, the upper pair lanceolate or elliptic-lanceolate to oblanceolate, 7-15 cm long, 3-6 cm wide, lower pairs lanceolate to elliptic-lanceolate, strongly unequal, the upper half tapering abruptly towards the tip, the lower-

most pair 3-5 cm long, 1-3 cm wide; rhachis terete, sometimes winged in the upper interfoliolar sections, 8-18 cm long, often ending in a linear appendix about 4 mm long, densely tomentose, the glands urceolate to scutellate, up to 2 mm in diam; petiole terete, 1-2 cm long, densely tomentose, the pulvinus conic and thicker. *Inflorescences* axillary, solitary or in groups of 2-4; peduncle 3-4 cm long, densely tomentose; rhachis 1.5-3.5 cm long, the bracts small, spathulate, about 1 mm long, thick and pubescent in the back. *Flowers* sessile, in compact spikes; calyx tubular, 3-4 mm long, tomentose, the teeth minute and irregular; corolla tubular, 16-20 mm long, sericeous-villose, the lobes acute, up to 3 mm long; staminal tube included. *Legume* flat, rounded at the ends, apiculate, 6-18 cm long, about 2 cm wide, gray or ferrugineous-pubescent, the borders elevated.

Lowlands from British Honduras to Panama; Trinidad. (South America.)

Vernacular names: *tama tama, mountain bribri* (British Honduras).

British Honduras: Big Creek, *Schipp 19* (F, GH, MO, NY, US); Middlessex, *Hope 111* (F), *Schipp 385* (F, GH, MO, NY); Monkey River, Toledo District, *Gentle 3691* (MO, NY), *3959* (MO, NY, US); Pine Ridge, *Bartlett 11683* (GH, NY, US); Silk Grass Forest, *Burns 25* (F, NY, US), *Gentle 2988* (NY); Temash River, *Schipp 1363* (F, GH, MO, NY, US); without locality, *Peck 496* (GH, K).

Guatemala: alta verapaz: Gubilgüitz, *Tuerckheim 4090* (NY, US); Sepacuité, *Cook & Griggs 641* (US), *729* (US), *734* (US); Yaxcabnal, Gubilgüitz, *Steyermark 45095* (F). izabal: Bananera to La Presa, *Steyermark 38108* (F); Cerro San Gil, *Steyermark 39480* (F); Livingston, *C. L. Wilson 361* (F); Los Andes to Entrerrios, *Record 40* (GH, US); Puerto Barrios, *Standley 73046* (F); valley of Motagua, *Steyermark 38985* (F); Virginia to Lago Izabal, *Steyermark 38844* (F). without locality: *Lewton 418* (US).

Honduras: colon: Guarunta, *von Hagen 1345* (F, NY).

Costa Rica: cartago: Moravia, Turrialba, *Córdoba 331* (IAIAS). san jose: El General, *Dayton & Barbour 3128* (US), *Skutch 2518* (MO, NY), *4232* (MO, NY, US).

Panama: canal zone: Barro Colorado Island, *Shattuck 1122* (F), *Zetek 3834* (F); Frijoles, *Standley 27581* (US), *27588* (US), *Stevens 1272* (ILL).

Trinidad: Aripo road, *Broadway 5789* (MO); Caroni, *Eggers 1383* (US); Dibe valley, *Britton & Coker 1756* (GH, US); Maraval, *Britton & Hazen 1593* (GH), *Hart 5818* (US); Sangre Grande, *R. O. Williams 11853* (US). without locality: *Trinidad Bot. Gard. Herb. 2841* (US).

This species is remarkable for the variability in the shape of the leaflets even of trees growing side by side, to which attention has been called by the collectors in Brazil, the Guianas and British Honduras. Herbarium specimens of *I. thibaudiana* are very often identified as *I. multijuga* Benth., a related Central American species.

16. Inga skutchii Standley, Publ. Field Mus. Nat. Hist., Bot. Ser., **23:** 11, 1943. (Type *Skutch 4823*)

Trees about 9 m tall; branchlets terete, densely ferrugineous-tomentose to glabrescent. *Leaves* with 6-8 pairs of leaflets; leaflets elliptic to ovate, the apex obtuse, ending in a short, pilose mucro, the base obtuse to rounded, above glabrous except along the costa, the nerves slightly marked, the margin undulate and sparsely pilose, beneath paler, very sparsely pilose, the nerves prominent, the upper pair elliptic, 4-7 cm long, 1-2 cm wide, the basal pair lanceolate, 2-3 cm long, 1.0-1.5 cm wide, the petiolule about 1 mm long, densely pilose; rhachis terete,

slender, 4-9 cm long, densely yellow-pilose, the glands small, hemispheric, about 0.5 mm in diam, pertuse and glabrous at the apex; petiole terete, 1 cm long, densely pilose, the pulvinus conic; stipules lanceolate, 2 mm long, pilose. *Inflorescences* 1-3, axillary; peduncle slender, terete, 3-4 cm long, tomentose; rhachis 5-7 cm long, the bracts minute, lanceolate, about 3 mm long, pubescent, persistent. *Flowers* sessile or shortly pedicellate, distant, irregularly arranged on the rhachis; calyx tubular, cleft on two sides, 5-6 mm long, striate, sparsely pilose, the teeth irregular, minute, more pilose; corolla tubular-funnelform, 15-18 mm long, appressed-pilose, the lobes acute, 2 mm long; staminal tube included, the filaments about 1.5 cm long. *Legume* unknown.

Forests of western Costa Rica.

COSTA RICA: SAN JOSE: basin of El General, *Skutch* 4823 (CR, F, MO).

Noteworthy for the slender rhachises, both in the leaves and in the inflorescences and for the very distant flowers; it is close to the Panamanian *I. multijuga* and its Costa Rican variant, *I. aestuarium,* from which it differs in the loose inflorescence and deeply cleft calyx.

17. INGA RUIZIANA G. Don, Gen. Hist. Dichl. Pl. **2:** 391, 1832. (Type *Ruiz* 5)

I. fagifolia G. Don, loc. cit., non Willd. (*fide* Bentham).
I. foliosa Benth. in Hook., Lond. Jour. Bot. **4:** 597, 1845 (*fide* Bentham).
Feuilleea ruiziana (G. Don) O. Ktze., Rev. Gen. Pl. **1:** 189, 1891.
Inga confusa Britton & Rose, N. Amer. Flora **23:** 5, 1928. (Type *Pittier* 5533)

Trees up to 25 m tall; branchlets terete, lenticellate; with minute, appressed and ferrugineous pubescence. *Leaves* with 4-8 (generally 6-7) pairs of leaflets; leaflets obovate to ovate, sometimes asymmetric, the apex acute or acuminate, often ending in a short and strong mucro, the base acute, oblique or rounded, above slightly pilose to glabrous, the nerves impressed, beneath puberulent, the nerves reticulate and prominent, the upper pair obovate-elliptic, 15-34 cm long, 5-12 cm broad at the wider section, lower leaflets elliptic to ovate, the basal pair 3-6 cm long, 3-4 cm wide; rhachis angulate, sometimes marginate in the upper sections, 8-28 cm long, ferrugineous-puberulent, the glands sessile, patelliform, 1-2 mm in diam; petiole terete, 1-2 cm long, densely ferrugineous-puberulent, the pulvinus short and thick; stipules lanceolate, up to 5 mm long, ferrugineous-pubescent, caducous. *Inflorescences* axillary on the old wood or paniculate on the new growth, in numerous clusters of 2-4 spikes each, peduncle slender, 2.5-4.0 cm long, densely ferrugineous-pubescent; rhachis 1.0-1.5 cm long, the bracts linear, acute, 1.5 mm long. *Flowers* sessile, appressed; calyx subturbinate, 3-5 mm long, sparsely pilose, the teeth acute and small; corolla tubular, 7-9 mm long, strigose, the lobes acute, somewhat spreading, 1.0-1.5 mm long; staminal tube included, the filaments about 1 cm long. *Legume* flat, oblong, slightly curved, 8-16 cm long, 2-4 cm wide, woody, the margins elevated.

Wet lowlands of Nicaragua to Panama. (Colombia to Peru and Brazil.)

NICARAGUA: CHONTALES: Castillo Viejo, *Shimek & Smith* 535 (EAP). SAN JUAN DEL NORTE: San Juan del Norte, *C. L. Smith* 7 (EAP, GH, MO).

Costa Rica: cartago: Atirro, *León 3962* (IAIAS); Instituto de Ciencias Agrícolas, *Córdoba 89* (IAIAS), *Holdridge 2560* (IAIAS), *León 1828* (IAIAS); Juan Viñas, *Cook & Doyle 391* (US); Las Vueltas, Tucurrique, *Tonduz 13054* (CR, GH, K, NY, US); Pejivalle, *Skutch 4607* (CR, F, MO, NY, US); Santa Rosa, Turrialba, *León 1520* (EAP, IAIAS); Tuis, *Córdoba 135* (IAIAS, MO). limon: Limón, *Tonduz 9801* (CR, US); Río Hondo, *Pittier 16646* (US); Shirores, *Tonduz 9356* (CR). puntarenas: Río Esquinas, *Allen 5842* (EAP). san jose: El General, *Skutch 2895* (GH, MO, NY, US), *3834* (MO, NY, US).

Panama: bocas del toro: Chiriquí Lagoon, Punta Rovalo, *Seibert 1558* (MO); Old Bank Island, *von Wedel 2012* (GH, MO); Shepherd Island, *von Wedel 2677* (GH, MO); Water Valley, *von Wedel 844* (GH, MO). canal zone: Barro Colorado Island, *Avilés 70* (F), *112* (F), *Brown 95* (F), *Bangham 516* (F), *Shattuck 468* (F), *C. L. Wilson 4* (F), *Zetek 3826* (F), *3839* (F); Gamboa, *Pittier 6520* (GH, NY, US); Masambi, *Pittier 2674* (GH, NY, US); Obispo, *Standley 31678* (US), *31690* (US); Quebrada Salamanca, *Dodge, Steyermark & Allen s. n.* (MO). colon: Río Fató, *Pittier 3917* (NY, US). darien: Marraganti *R. S. Williams 768* (NY); Río Sambú, *Pittier 5533* (GH, NY, US).

A species which is well marked by its obovate upper leaflets and congested inflorescences generally at the end of new growth. There is no apparent reason to segregate the Central American trees into a different species as was done by Britton & Rose.

Planted often in Costa Rica and Panama as shade trees in the lower coffee belt or in the cacao grove at below 600 m elevation.

Series 3. **DENSIFLORAE** J. León, ser. nov.

Arbor; ramuli teretes vel angulati. *Folia* foliolis generaliter 4 minusve; rhachis plerumque alata; petiolus curtus. *Inflorescentiae* 1-4; pedunculus rhachisque curta bracteis linearibus vel lanceolatis. *Flores* sessiles congesti. *Legumina* plana marginibus laete elevatis.

Trees; branchlets terete or angulate, generally pubescent. *Leaves* with a low number of pairs of leaflets, generally 4 or less; leaflets pubescent to glabrous, thin, flat; rhachis commonly winged, but extremely variable even in the same species, often marginate; petiole short, winged or terete. *Inflorescences* 1-4, axillary or terminal, in one case on the old wood; peduncles short, stout or filiform; rhachis short, the bracts linear to lanceolate. *Flowers* sessile, congested; calyx short, tubular, pilose; corolla tubular, appressed-pilose. *Legume* flat, quite variable in size, the margins slightly elevated, sparsely pilose to glabrescent.

Type species: *I. densiflora* Benth.

Species of the series densiflorae are characterized by large, thin leaves with few pairs of leaflets and large, flat legumes. Its center of variation occurs in northern South America on the two sides of the Andes (see under *I. densiflora*). The Central American species form a highly complex unit, in which *I. schiedeana, I. micheliana* and *I. davidsoniae* may be only variants of *I. densiflora.* On the other hand there are several endemics with no clear relationships, such as *I. stenophylla, I. barbourii, I. hintoni.*

The densiflorae form a connection between the punctatae and the other series of this section.

species . . . 18-27

a. Branchlets, leaves and legumes sparsely pilose to glabrous.
 b. Peduncle stout, pubescent or glabrous; leaves large, the upper leaflet more than 3 cm wide.
  c. Branchlets, leaves and peduncles pilose or pubescent; legume pilose or glabrous.
   d. Leaflets 4-6 pairs; corolla 5-8 mm long.
    e. Bracts linear lanceolate, 3-4 mm long. Panama, Costa Rica ....18. I. DENSIFLORA
    ee. Bracts linear, 4-9 mm long. Mexico ....19. I. SCHIEDEANA
   dd. Leaflets 3 pairs; corolla 9 mm long. Guatemala ....20. I. MICHELIANA
  cc. Branchlets, leaves and peduncles glabrous; legume glabrous or covered with scales.
   f. Leaves thin, 5-6 pairs of leaflets; upper pair 11-14 cm long; legume white-lenticellate. Costa Rica ....21. I. SQUAMIGERA
   ff. Leaves coriaceous; 4 pairs of leaflets; upper pair 8 cm long; legume sparsely pilose. Panama ....22. I. DAVIDSONIAE
 bb. Peduncles filiform, sparsely pilose to glabrous; leaves small, the upper pair less than 3 cm wide.
  g. Upper leaflets oblong-lanceolate to falciform, 1.0-1.5 cm wide, acute at the apex; rhachis terete to marginate. Costa Rica ....23. I. STENOPHYLLA
  gg. Upper leaflets elliptic to oblong, 2-3 cm wide, clearly mucronate; rhacis marginate to broadly winged.
   h. Inflorescences in short spurs; corolla 6-7 mm long; leaflets glossy. Mexico ....24. I. TENUIPEDUNCULATA
   hh. Inflorescences axillary; corolla less than 4 mm long; leaflets opaque. Costa Rica ....25. I. BARBOURII
aa. Branchlets, leaves and legumes densely ferrugineous pilose.
 i. Calyx 3-5 mm long; leaves bullate. Legume thin. Mexico ....26. I. HINTONI
 ii. Calyx 7-9 mm long; leaves flat; legume thick. El Salvador-Mexico ....27. I. CALDERONI

18. INGA DENSIFLORA Benth., Trans. Linn. Soc. **30:** 617, 1875. (Type *Spruce 4504*)

I. langlassei Pittier, Contr. U. S. Nat. Herb. **18:** 189, 1916. (Type *Langlassé 63*)
I. mollifoliola Pittier, loc. cit. (Type *Pittier 3251*)
I. monticola Pittier, loc. cit. 190. (Type *R. S. Williams 316*)
I. sordida Pittier, loc. cit. 191. (Type *Lehmann 904*)
I. montealegrei Standley, Publ. Field Mus. Nat. Hist., Bot. Ser., **18:** 1154, 1938. (Type *Montealegre 1*)

Trees; branchlets terete, striate, densely yellow-tomentose when young, in age glabrate and lenticellate. *Leaves* with 4-6 (generally 4) pairs of leaflets; leaflets asymmetric, oblong to obovate, the apex acute to acuminate, sometimes mucronate, the base oblique, acute to rounded, above lustrous or dull, sparsely pilose to glabrous, the nerves prominent and more pubescent, beneath paler, densely to sparsely pilose, the nerves prominent with conspicuous reticulate nervation, the upper pair elliptic to obovate-elliptic, 7-18 cm long, 3.5-7.0 cm wide, the basal pair lanceolate-elliptic, 2.5-4.0 cm long, 1.5 cm wide, the petiolule very short, 1 mm long, pilose; rhachis marginate to slightly winged above, terete below, 5-10 cm long, yellow-pilose, especially on the midnerve, ending in a linear and pilose appendix, the glands patelliform, black, 1.5-2.0 mm in diam; petiole terete or marginate above, 1-2 cm long, densely yellow-pilose, the pulvinus conic, fleshy and black; stipules subulate, 2-5 mm long, striate, caducous. *Inflorescences* axillary, 2-4; peduncle terete, 4-6 cm long, striate, pilose; rhachis short, 1-3 cm long, the bracts linear-lanceolate, 3-4 mm long, pilose, semi-persistent. *Flowers* congested,

sessile; calyx tubular, 2.5-5.0 mm long, sparsely pilose to glabrate above, densely pilose at the base, the teeth small, irregular, 1.0-1.5 mm long; corolla tubular, widening towards the apex, 6.5-9.0 mm long, appressed-pilose, the lobes acute, about 1 mm long; staminal tube included. *Legume* flat, oblong, 8-22 cm long, 3-8 cm wide, finely pilose when young, in age glabrate, transversely striate, the borders elevated.

Costa Rica to Panama. (Northern South America.)

Costa Rica: alajuela: La Palma, San Ramón, *Brenes 6805* (CR, F, IAIAS), *19001* (CR, F); La Paz, San Ramón, *Córdoba 180* (IAIAS); Palmares, *Córdoba 190* (IAIAS); Piedades, San Ramón, *Brenes 5459* (CR, F, IAIAS), *5469* (CR, F), *5842* (CR, F); San Isidro, San Ramón, *Córdoba 182* (IAIAS), *183* (IAIAS), *184* (IAIAS), *185* (IAIAS); San Miguel a La Palma, San Ramón, *Brenes 17049* (CR, F); San Pedro, San Ramón, *Brenes 4341* (CR, F), *4673* (CR, F), *4676* (F), *4826* (F), *4843* (F), *5002* (F), *6634* (CR, F), *19456* (CR, F, IAIAS), *19479* (CR); San Ramón, *Córdoba 181* (IAIAS); Santiago, San Ramón, *Brenes 17186* (CR, F). cartago: Atirro, *León 1921* (IAIAS); Instituto de Ciencias Agrícolas, *Córdoba 91* (IAIAS), *Holdridge 2550* (IAIAS), *León 1850* (EAP, IAIAS); Santa Rosa, Turrialba, *León 2448* (EAP, IAIAS). san jose: Pavas, *Montealegre 1* (CR, F), *2* (CR, F); Rodeo de Pacaca, *Pittier 3251* (CR, US); San Marcos de Dota, *Tonduz 7548* (CR).

Panama: cocle: Bismarck, above Penonomé, *R. S. Williams 316* (US). san blas: Permé, *G. P. Cooper 651* (F, NY, US).

Inga densiflora is one of the most variable species in the genus. In Costa Rica it is very commonly planted as a shade tree in the coffee fields of the highlands; the populations in that area are distinguished by the dense tomentum and short leaflets. The type most common in the coffee fields (*I. montealegrei*) has more glabrous and larger leaflets. The populations are so variable that they are assigned different specific names in the herbaria. The numerous collections made by Brenes, and large local samples taken by the author, show all sort of intergradations among these populations (i.e., broadly winged to slightly marginate rhachises, etc.). In the present treatment, two species of northern Central America are maintained because of the lack of intergrading materials. But it is possible that future collections may prove that *I. micheliana, I. schiedeana* and the Panamanian species *I. davidsoniae* are only aberrant populations of *I. densiflora.*

It is necessary to point out that *I. densiflora* has a series of more complex populations in northern South America. In Colombia they receive several names: *I. sordida* Pittier, *I. langlassei* Pittier, *I. microdontha* Britton & Killip, *I. tiribiana* Britton & Killip, etc. All of them show a remarkable similarity among themselves and with the type specimen of *I. densiflora* at Kew. In Venezuela *I. heinei* Harms and *I. limonensis* Pittier also belong to the group mentioned above, while *I. java* Pittier, as noted by Schery (Ann. Missouri Bot. Gard. **37:** 196, 1950), is similar to many Central American specimens. Types of the above taxa were studied.

19. Inga schiedeana Steud., Nom. Bot. **1:** 810, 1840. (Based on *I. flexuosa* Schlecht., non Graham)

I. flexuosa Schlecht., Linnaea **12:** 559, 1838, non Graham. (Type *Schiede 674*)
I. pringlei Harms in Fedde, Rep. Sp. Nov. **13:** 526, 1915. (Type *Pringle 8125*)

Small *trees;* branchlets terete or angulate, densely ferrugineous-puberulent when young, in age glabrate and lenticellate. *Leaves* with 4-6 (generally 5) pairs of leaflets; leaflets oblique, obovate-elliptic to lanceolate, the apex acute to acuminate, the base cuneate to rounded, often asymmetric, above opaque to sublustrous, sparsely pubescent and more densely on the costa and margin, the nerves prominent, beneath paler, sparsely pilose, the lateral nerves and reticulate nervation prominent, the upper pair elliptic-obovate, often oblique, 6-9 cm long, 2.0-3.5 cm wide, the basal pair considerably smaller, lanceolate to elliptic, 2-5 cm long, 1-2 cm wide, the petiolules very short, densely ferrugineous-pubescent; rhachis winged, the wings often restricted to the upper interfoliolar sections, 6-10 cm long, the glands minute, crateriform, glabrous; petiole terete, 1.0-1.5 cm long, densely ferrugineous-puberulent. *Inflorescences* axilliary or terminal, solitary or in groups of 2-3; peduncle terete, 3-5 cm long, densely ferrugineous-tomentose; rhachis 2.5-3.0 cm long, the bracts linear-lanceolate, 4-9 mm long, pubescent. *Flowers* sessile, congested, soon deciduous; calyx conic, cleft on two sides, 6-7 mm long, striate, sparsely pilose, the teeth irregular, 1-2 mm long, more pilose; corolla tubular, 7-8 mm long, appressed-pilose, the lobes acute, 1.5 mm long; staminal tube included. *Legume* unknown.

Highlands of Veracruz, Mexico.

MEXICO: VERACRUZ: Jalapa, *Pringle 8125* (F, GH, MO), *Schiede 674* (GH).

Inga schiedeana is very closely related to *I. densiflora* of southern Central America. Neither of these species has been reported from Guatemala to Nicaragua.

20. INGA MICHELIANA Harms in Fedde, Rep. Sp. Nov. **13:** 525, 1915. (Type *Heyde & Lux 3319*)

Trees; branchlets terete or angulate, minutely puberulent when young, in age glabrate. *Leaves* with 3 pairs of leaflets; leaflets subchartaceous, elliptic to lanceolate, the apex obtuse, ending in a short mucro, the base cuneate, obtuse or rounded, above lustrous, sparsely pilose, the nerves prominent and more densely pubescent, beneath paler, densely pilose, the nerves conspicuous; the upper pair elliptic, oblique, 5.5-7.5 cm long, 2.5-1.5 cm wide, the petiolules very short and pilose; rhachis winged, 3-6 cm long, pilose especially on the midnerve, the glands crateriform, glabrous; petiole terete, about 1.5 cm long, densely ferrugineous-puberulent. *Inflorescences* axillary, solitary or geminate; peduncle 2.5-4.0 cm long, ferrugineous-tomentose; rhachis about 1.5 cm long, the bracts minute, ovate, about 1 mm long, densely pubescent. *Flowers* sessile, congested; calyx tubular, 5 mm long, pilose, the teeth small, irregular, 0.5-1.0 mm long; corolla tubular, 9-11 mm long, densely appressed-pilose, the lobes acute, 1.5 mm long; staminal tube included. *Legume* unknown.

Highlands of northern Guatemala.

GUATEMALA: QUICHE: Río Negro, *Heyde & Lux 3319* (GH, MO).

Definitely known only from the type collection; the small size of the bracts and shape of the calyx help to separate it from the Mexican *I. schiedeana.*

21. INGA **SQUAMIGERA** J. León, sp. nov.

Arbor 8-15 alta; ramulis angulatis glabris dense lenticellatis. *Foliola* plerumque 5-6-juga (rariore 4-7) elliptica vel oblonga, apice late acuminata mucro 1 mm longo, basi obtusa, assimetrica, supra glabra nitida viridia opaca vel glauca, subtus pallidioria glabra nervis prominentibus, superioria oblonga vel elliptica 11-14 cm longa 5-6 cm lata, media elliptco-oblonga 8-14 longa 3-4 cm lata, inferioria lanceolata 5-9 cm longa 2-3 cm lata, petiolulis 1 mm longis pilosis; rhachibus marginatis 10-18 cm longis pilosis, glandulis interfoliolaribus patelliformibus circa 2 mm diametralis foramine profundo; petiolis marginatis vel teretibus glabrescentibus 3-4 mm longis; stipulis linearibus 7 mm longis caducis. *Inflorescentia* ignota. *Legumen* oblonga lata vel recurvata marginibus prominentibus 12-16 cm longa 4-5 cm lata transverse striata junior pallide lenticellata glabrescens.

Trees, 8-15 m tall, with an open crown; branchlets angulate, densely lenticellate, glabrous. *Leaves* with 4-7, generally 5-6 pairs of leaflets; leaflets lanceolate to elliptic, asymmetric, undulate, the apex abruptly acuminate, shortly mucronate, the base obtuse, strongly asymmetric, the lower side narrower in the median and upper leaflets, above light green, lustrous, completely glabrous, the lateral nerves slightly prominent, beneath paler, glabrous, the costa and lateral nerves prominent and sparsely pilose, borders markedly undulate, the upper pairs oblong 11-14 cm long, 5-6 cm wide, the median pairs elliptic-oblong 8-14 cm long, 3-4 cm wide, the lower pair lanceolate 5-9 cm long, 2-3 cm wide, the petiole 1 mm long, pilose; rhachis marginate, canaliculate above, 10-18 cm long, very sparsely pilose, the glands patelliform, 1.5-2 mm diameter; petiole marginate, the pulvinus darker and thicker, 4-5 long; stipules linear, 7 mm long 2 mm wide, pilose, caducous. *Inflorescences* solitary or in groups of 2-4, on the old branches or on defoliated nodes of the branchlets. Peduncle thick, terete, densely brown, pilose, lenticellate, 0.1-1.0 cm long; rhachis thick, cylindric, pilose, 2-3 cm long, the bracteoles spathulate, pilose 2-3 mm long, semicaducous. *Flowers* unknown. *Legume* flat, elliptic, oblong, 12-16 cm long, 4-5 cm wide, 1.5-2.0 cm thick, transversely striate, the borders well developed, when young completely covered with white scales giving a striking appearance to the fruits, in age smooth and green. (The white, powdery scales, of variable size and shape, completely cover the fruits; mites and aphids are common among them.)

Wet lowlands of northern Costa Rica; planted as coffee shade in the San Carlos valley.

COSTA RICA: ALAJUELA: road to Upala, at La Bijagua, *Léon 4869* (CR, HOLOTYPE IAIAS, MO); Florencia de San Carlos, *Léon 5000* (IAIAS).

This species is closely allied to *I. densiflora,* differing in the completely glabrous foliage and in the almost white fruits lenticellate at early stages. It is frequent in forests and pastures and often planted as shade trees in the coffee fields of the San Carlos-Río Frío watershed, an area which has not been explored botanically.

22. Inga davidsoniae Standley, Publ. Field Mus. Nat. Hist., Bot. Ser., **22:** 79, 1940. (Type *Davidson 943*)

Trees 4-9 m tall, densely branched; branchlets terete, minutely tomentose to glabrescent, lenticellate. *Leaves* with 3-5 pairs of leaflets; leaflets coriaceous, distant, elliptic to ovate, the apex acute to obtuse, mucronate, the base rounded or obtuse, asymmetric, above sparsely pilose to glabrescent, glossy, the nerves impressed, beneath sparsely pilose to glabrescent, the main nerves prominent and pilose, the upper pair elliptic, up to 8 cm long, 4 cm wide, the intermediate elliptic to lanceolate, sometimes strongly asymmetric, the lower pair ovate, about 2.5 cm long, 1.5 cm wide, the petiolules short, pilose; rhachis narrowly winged or marginate, 2.0-7.5 cm long, pubescent on the midnerve, the glands conic or cupuliform, less than 1 mm long, glabrous; petiole terete, the pulvinar section black, 0.5-2.0 cm long, tomentose. *Inflorescences* axillary; peduncle about 3.5 cm long; rhachis about 1.5 cm long. *Flowers* unknown. *Legume* flat, oblong, straight or curved, truncate to apiculate at the apex, the base rounded, 11-12 cm long, 4 cm wide, the borders elevated.

Cloud forests of western Panama, at 2250 m elev; known only from the type collection.

Panama: chiriqui: Boquete, Volcán Chiriquí, *Davidson 943* (F, MO).

This imperfectly known species seems to be related to *I. densiflora* which is frequent at lower elevations. The glossy and glabrescent leaves are unusual in this genus.

23. Inga stenophylla Standley, Publ. Field Mus. Nat. Hist., Bot. Ser., **18:** 499, 1937. (Type *Brenes 6841*)

Trees; branchlets terete, lanose when young, in age glabrate, densely lenticellate. *Leaves* with 4-7 pairs of leaflets; leaflets subcoriaceous, oblong to linear-lanceolate, the apex straight to falcate, acuminate, the base oblique, acute, above deep green, lustrous, sparsely pilose, the pubescence more dense on the impressed nerves and margins, beneath paler, sparsely pilose to glabrous, the nerves slightly prominent, the upper pair oblique, oblong-lanceolate to falciform, 5-7 cm long, 1.0-1.5 cm wide, the lower pairs oblong-lanceolate, the basal pair 3.0-5.5 cm long, 1.0-1.5 cm wide, the petiolule very short, pilose; rhachis very narrowly winged in the upper interfoliolar sections, slender, 5-9 cm long, sparsely pilose to glabrous, the glands minute, shortly stipitate, glabrous; petiole terete, 1-2 cm long, the pulvinus conic. *Inflorescences* axillary on the old wood or paniculate on the young branchlets, the spikes solitary or in groups of 2-4; peduncle slender, 1-4 cm long, striate, densely pilose, sometimes with an empty bract in the upper part; rhachis angulate, 2.0-2.5 cm long, pilose, the bracts minute, lanceolate, about 1.5 mm long, densely pubescent, caducous. *Flowers* sessile, closely appressed; calyx campanulate, 2-3 mm long, pilose, the segments obtuse, about 1 mm long; corolla tubular, 6-7 mm long, pilose, the lobes acute, 1.0-1.5 mm long; staminal tube included, the filaments 1.0-1.5 cm long. *Legume* (immature) flat, oblong, acumi-

nate, 18-22 cm long, 1.0-1.5 cm wide, sparsely pilose, the borders elevated; seeds 9-15.

Highland forests of central Costa Rica.

Costa Rica: alajuela: La Calera, San Ramón, *Brenes 11574* (CR, F); La Palma, San Ramón, *Brenes 5802* (CR, F, IAIAS); Santiago, San Ramón *Brenes, 6707* (CR, F, IAIAS), *6841* (CR, F, IAIAS); San Ramón, *Brenes 382 [566]* (F, US). san jose: Tarbaca, *León 3829* (MO, IAIAS).

In *I. stenophylla* the leaf rhachis varies from winged to almost terete; in this and the floral characters the position of this species seems to be intermediate between this series and the series punctatae.

24. Inga **tenuipedunculata** J. León, sp. nov.—Fig. 3.

Arbor 15-24 m alta; ramulis teretibus glabris dense lenticellatis. *Foliola* plerumque 4-(rarius 5-)juga elliptica vel lanceolata, apice late acuminata mucro lineari ca 1.5 mm longo, basi acuta oblique, supra saturate viridia opaca sparsissime pilosa vel glabra costa nervisque lateralibus prominentibus et pilosioribus, subtus palliodoria pilosa vel glabra nervis gracilibus prominentibus, superiora anguste elliptica 5-9 cm longa 2-3 cm lata, inferiora lanceolata vel ovata 1.5-2.0 cm longa 0.7-1.0 cm lata, petiolulis ca 1 mm longis pilosis; rhachibus alatis 4-8 cm longis costa dense pilosis, alis anguste oblongis 2 mm latis glabris, glandulis interfoliolaribus tenuis elevatis 2-3 mm longis glabris foramine profundo; petiolis teretis vel alatis 1.0-1.5 cm longis glabrescentibus, pulvino crassiori glabro; stipulis anguste lanceolatis ca 4 mm longis ciliatis subpersistentibus. *Inflorescentiae* in ramulis brevibus lateralibus paniculatae; pedunculis filiformibus teretibus 3-6 cm longis sparse pilosis; rhachibus ca 2 cm longis, bracteis lanceolatis 1 mm longis pilosis deciduis. *Flores* sessiles remoti; calyce tubuloso 3-4 mm longo, dentibus obtusis minutis; corolla tubulosa infundibuliformi 6-7 mm longa appresse pilosa, lobis acutis ca 2 mm longis; tubo staminali incluso. *Legumen* ignota.

Lowlands of Veracruz, Mexico.

Vernacular names: *acotopillo, frijolillo* (Veracruz—Ll. Williams).

Mexico: veracruz: Fortuño, Coatzacoalcos River, *Ll. Williams 8935* (F), *9029* (F, holotype NY).

Inga tenuipedunculata has no close ally in Central America. It is very similar to *I. acuminata* Benth. in leaflet shape, the type of narrow wings in the rhachis and the position of the inflorescences on short spurs. It lacks, however, the congested inflorescences and irregular calyces which characterize *I. acuminata.*

25. Inga barbourii Standley, Publ. Field Mus. Nat. Hist., Bot. Ser., **23:** 55, 1944. (Type *Barbour 1008*)

Trees to 20 m tall; branchlets terete, puberulent to glabrescent, densely lenticellate. *Leaves* with 4-6 pairs of leaflets; leaflets elliptic to lanceolate, the apex acute to acuminate, ending in a straight and short mucro, the base acute to rounded, above sublustrous, sparsely pilose to glabrous, the costa prominent and

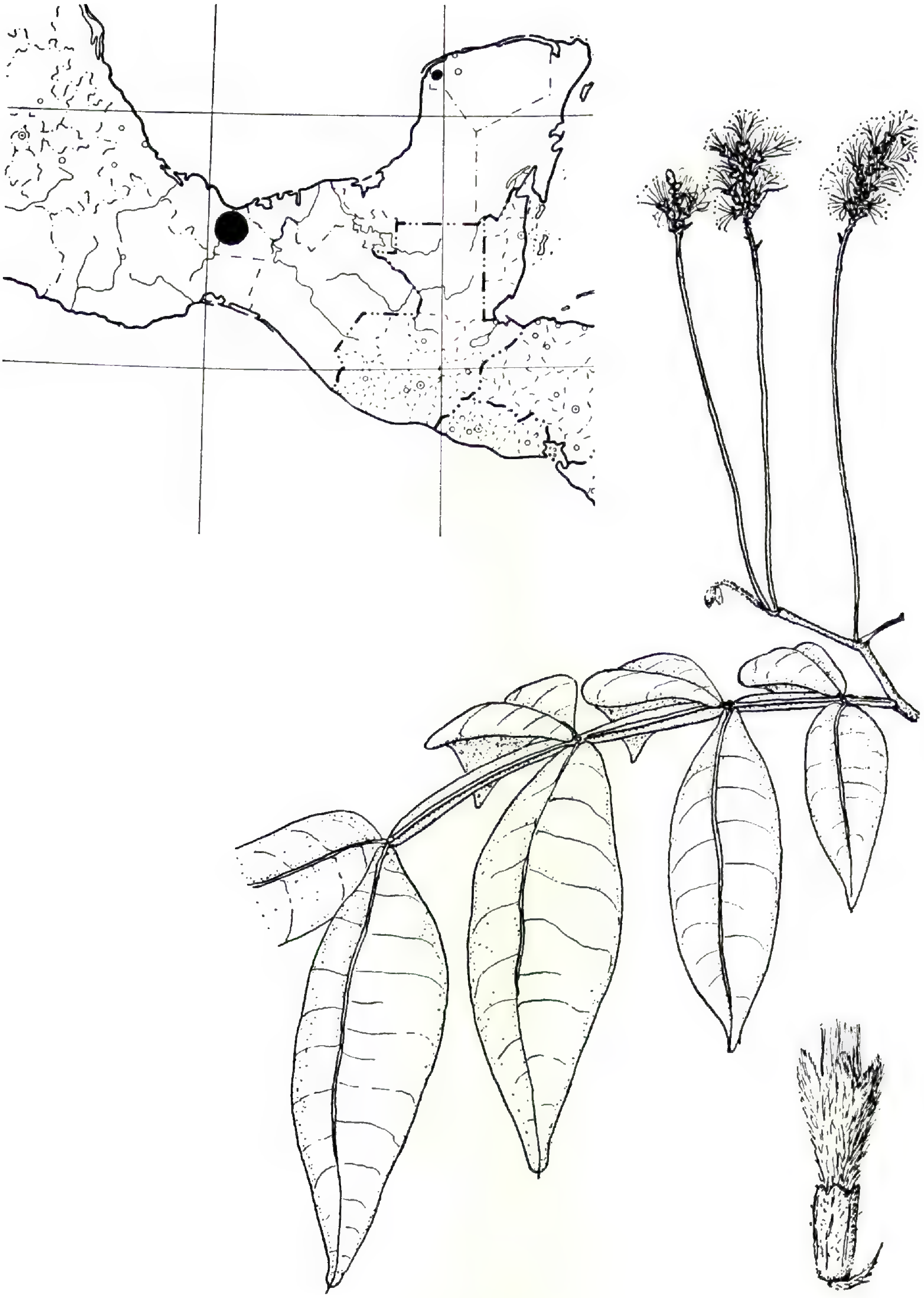


Fig. 3. *Inga tenuipedunculata* J. León

more pilose, the lateral nerves inconspicuous, beneath sparsely pilose, the margin pilose, the main nerves prominent and more pubescent, the nervation finely reticulate and conspicuous, the upper pair elliptic, 6-9 cm long, 2-3 cm wide, the basal pair lanceolate-elliptic, 1.5-2.0 cm long, 0.7-1.5 cm wide, the petiolule very short and pilose, giving a sessile appearance to the leaflets; rhachis narrowly and elliptically winged, 3-5 cm long, pilose especially along the midnerve, the glands small, crateriform, glabrous; petiole terete or marginate, 0.5-1.5 cm long, densely ferrugineous-puberulent when young, in age glabrate, the pulvinus thick and darker; stipules lanceolate, 2 mm long, pilose, deciduous. *Inflorescences* 1-4, axillary on the new growth; peduncle terete, filiform, 1-3 cm long, sparsely pilose; rhachis 0.7-1.0 cm long. *Flowers* minute, sessile, congested; calyx tubular, 2-3 mm long, pilose; corolla tubular, 5-6 mm long appressed-pilose. *Legume* flat, oblong, the apex rounded and ending in a short acumen, the margins elevated, the base rounded, 5-6 cm long, 1 cm wide, sparsely pilose to glabrescent.

Costa Rica: alajuela: Puente La Vieja, San Carlos, *León 3578* (IAIAS). cartago: Pavones, Turrialba, *Barbour 1008* (CR, F); Río Tuis, *León 3842* (IAIAS, MO).

An endemic species not uncommon in the wet subtropical forests of Costa Rica between 500-600 m elevation; it is a large tree, with loose foliage, rather attractive for its small, light green leaves.

These trees do not bloom as often as other species. Several plants were observed for four years without showing any signs of flowers, in spite of the production of several flushes every year.

26. Inga hintoni Sandwith, Kew Bull. **1937:** 304, 1937. (Type *Hinton 7617*)

Trees 5 to 12 m tall; branchlets terete, densely ferrugineous-pilose in the young growth, in age glabrate and lenticellate. *Leaves* with 3-6 pairs of leaflets, the terminal pairs with a trend to congestion; leaflets chartaceous, slightly bullate, elliptic to ovate, the apex obtuse, mucronate, the base slightly oblique, rounded, above lustrous, glabrous to sparsely pilose on the main nerves and margins, the nerves well impressed, beneath glabrous to sparsely pubescent, the nerves prominent and pilose, the upper pair elliptic to elliptic-lanceolate, 3-15 cm long, 1.5-5.0 cm wide, the lower pairs considerably smaller, lanceolate to oval-lanceolate, the basal pairs 1.5-5.5 cm long, 1-3 cm wide, the petiolule short, about 1 mm long, conic, dark, pubescent; rhachis winged, 2.0-5.5 cm long, sparsely pubescent, the wings cuneate to rhombic, each up to 6 mm wide, the glands small, cupuliform, pertuse at the apex, about 0.5 mm long, the terminal appendix linear, 2 mm long, pilose; petiole terete, 0.7-1.5 cm long, densely ferrugineous-pubescent, the pulvinus conic and darker, 2-3 mm long; stipules small, triangular, 2-3 mm long, persistent. *Inflorescences* axillary, solitary or in groups of 2-3, peduncle slender, 2.0-3.5 cm long, ferrugineous-pubescent; rhachis 1.5-3.0 cm long, the bracts linear-spathulate, up to 2 mm long, pilose. *Flowers* sessile or shortly pedicellate, congested; calyx campanulate, cleft on one side, 3 mm long, pilose, the teeth irregular, 1.0-1.5 mm long, densely pilose towards the tips; corolla funnelform, 5-6 mm long, pilose, the lobes acute, 1.5-2.0 mm long; staminal tube included; ovary glabrous.

Legume flat, oblong, mucronate at the apex, 4-14 cm long, 1.5-2.5 cm wide, ferrugineous-pubescent to glabrate in age, the margins elevated.

Highlands of Mexico, from Michoacan to Chiapas.

Vernacular name: *jaquinicuil* (Mexico—Hinton).

MEXICO: CHIAPAS: Buena Vista, Escuintla, *Matuda 1899* (K, NY, US); Cascadas, Siltepec, *Matuda 5158* (EAP, F). MEXICO: Nanchititla, Temascaltepec, *Hinton 6171* (MO, US), 7617 (US), *7667* (F), *8103* (MO, US), *8232* (F, GH, MO, NY, US); Temascaltepec, *Hinton 4182* (MO, US), *8978* (GH, MO, NY, US); Rincón, Temascaltepec, *Hinton 456* (GH), *11202* (F, GH). MICHOACAN: Hacienda Coahuayula, *Emrick 48* (F).

This species, well known in central Mexico for its edible pods, is generally found above 1500 m elevation.

27. INGA CALDERONI Standley, Jour. Wash. Acad. Sci. **13:** 352, 1923. (Type *Calderón 1392*)

Low *trees,* up to 8 m tall; branchlets terete, densely fulvous-hispid, in age glabrous and lenticellate. *Leaves* with 4-7 pairs of leaflets; leaflets asymmetric, lanceolate to elliptic, the apex narrower, sometimes curved, acute to acuminate, the base rounded to oblique, asymmetric, above fulvous-pilose, the nerves impressed, beneath dull, more densely pilose, the nerves prominent, the upper pair lanceolate to elliptic, 6-9 cm long, 2.0-2.5 cm wide, the lowermost pair 2-4 cm long, 1.0-1.5 cm wide; rhachis winged, 5-8 cm long, pilose, the wings cuneate, broader towards the apical end, sometimes lacking in the lower sections, the glands long pedicellate, the pedicel slender, 2-4 mm long, pilose, pertuse and glabrous at the apex; petiole terete, 0.5-1.0 cm long, densely fulvous-pilose. *Inflorescences* solitary, axillary; peduncle terete, 2-3 cm long, pilose; rhachis 2.5-5.5 cm long, the bracts linear, 10-12 mm long, 1-2 mm wide, densely pilose, caducous. *Flowers* dense, sessile; calyx tubular 6-14 mm long, striate, densely pilose to glabrescent, the teeth acute, 1-2 mm long; corolla tubular, spreading above, 12-14 mm long, appressed-pilose; staminal tube included, the filaments about 2.5 cm long. *Legume* oblong, thick, 5-10 cm long, 3.0-3.5 cm wide, about 1 cm thick, markedly apiculate, the base rounded, densely ferrugineous-tomentose, the margins elevated; seeds large, surrounded by an edible aril.

Dry lowlands of western Central America from Mexico to Salvador.

Vernacular name: *pepeto de mico* (Salvador—Calderón).

MEXICO: CHIAPAS: Sta. Rosa, Escuintla, *Matuda 4236* (F, MO, NY, US).
GUATEMALA: SACATEPEQUEZ: Barranco Hondo, *Standley 88950* (F, US).
SALVADOR: AHUACHAPAN: Sierra de Apaneca, Finca Colima, *Calderón 20186* (GH). LA LIBERTAD: Comasagua, *Calderón 1392* (GH, US); Santa Tecla, *Calderón 1513* (GH, US), *Standley 23018* (NY, US).

Pittier included this species with his EUINGA-TETRAGONAE on account of the fruits; these and the floral characters, as well as the glands, however, are more close to those of the series DENSIFLORAE where it is here provisionally placed until better flowering material may clear its definite position.

Series 4. LEPTANTHAE Benth. in Hook., Lond. Jour. Bot. **4:** 602, 1845, emend.

Small *trees* or *shrubs.* Branchlets terete, hispid, in age glabrous. *Leaves* small, hispid, with 2-3 pairs of leaflets (in the Central American species); rhachis winged, with long-stipitate glands. *Inflorescences* 1-few; bracteoles lanceolate, pilose, persistent; calyx setose, the teeth subulate; corolla tubular appressed-pilose. *Legume* flat, ferrugineous-hispid.

The LEPANTHAE as here defined exclude some species, such as *I. acuminata,* which Bentham (Trans. Linn. Soc. **30:** 618, 1875) included in the group. This series is formed mainly by Brazilian species; the Guatemalan *I. cookii* is a remnant of a formerly widely distributed group. SPECIES . . . 28

28. INGA COOKII Pittier, Contr. U. S. Nat. Herb. **18:** 203, 1916 (Type *Cook & Griggs 505*)

I. subvestita Standley, Publ. Field Mus. Nat. Hist., Bot. Ser., **22:** 27, 1940. (Type *C. L. Wilson 315*)

Trees 3 to 8 m tall; branchlets terete, hispid or glabrescent. *Leaves* with 2-3 (rarely 4) pairs of leaflets; leaflets shortly petiolulate, obovate to ovate, acute to markedly acuminate at the apex, acute to obtuse and asymmetric at the base, above fulvous-pilose, with the nerves and costa deeply impressed and more pubescent, beneath densely fulvous-pilose, the main secondary nerves prominent and anastomosing close to the margin, leaving alternate and incomplete nerves between, the upper pair obovate to elliptic-obovate, 3-15 cm long, 2-7 cm wide, the basal pair ovate to elliptic, 2-7 cm long, 1-4 cm wide; rhachis winged, 1.5-12 cm long, hispid, the glands long and slenderly pedicellate, up to 2 mm long, glabrous and pertuse at the apex; petiole terete or winged, 0.5-8.0 cm long, hispidulous. *Inflorescences* axillary and solitary; peduncle slender, 3-8 cm long, setose; rhachis 1.5-3.5 cm long, pilose, the bracts lanceolate, 2-4 mm long, densely pilose, semipersistent. *Flowers* sessile or pedicellate; pedicel slender, up to 2 mm long, pilose; calyx tubular, 3-5 mm long, setose especially towards the tips, the lobes subulate, regular, separated by rounded sinuses, 1.0-1.5 mm long; corolla tubular-funnelform, 9-14 mm long, sparsely and long pilose, the lobes acute, 1.0-2.5 mm long, more pubescent; staminal tube included. *Legume* flat, oblong, 9-12 cm long, 4-5 cm wide, about 1 cm thick, densely ferrugineous-hispid, the margins not elevated.

Wet forests of Guatemala and Honduras, especially in the Caribbean watershed, from sea level to 1500 m elevation.

Vernacular name; *guamo de playa* (Honduras—Standley).

GUATEMALA: ALTA VERAPEZ: Campur to Socoyo, *Standley 91712* (F); Chirriacté, *Standley 91637* (F); Cobán, *Standley 69381* (F), *91544* (F), *92687* (F); Cobán to San Pedro Carchá, *Standley 89779* (F), *89988* (F); Cocolá, NE of Carchá, *Standley 70296* (F); Finca Transvaal, *C. L. Wilson 315* (F); Gubilgüitz, *Steyermark 44407* (F); Santa Cruz, Río Frío, *Standley 90207* (F); Santa Cruz to Tactic, *Standley 92277* (F); Sachaj, *Steyermark 45159a* (F); Sepacuité, *Cook & Griggs 103* (US), *202* (US), *226* (US), *505* (US). HUEHUETENANGO: Maxbal, *Steyermark 48852* (F). IZABAL: Bananera to La Presa, *Steyermark 38192* (F).

HONDURAS: ATLANTIDA: Tela, *Standley 54256* (US). COMAYAGUA: Siguatepeque, El Achiote, *Yuncker, Dawson & Youse 6292* (F, GH, MO), *6678* (GH).

Inga cookii is one of the most interesting species of this genus in Central America. Its closest allies are a group of Brazilian and Guianan species including *I. leptantha, I. ciliata,* etc. Especially striking are the type of setose indument found upon most parts of the plants, the peculiar calyx with subulate teeth, and the long and slender peduncles with acute, semi-persistent bracts subtending the rather distant flowers. The description of the fruit is based on the specimens from Siguatepeque, Honduras and, although lacking flowers, are similar to the most typical plants in foliar characters.

Series 5. ACUMINATAE J. León, ser. nov.

Arbor; ramuli teretes. *Folia* foliolorum paribus 6 minusve; rhachis alata. *Inflorescentiae* 1-aliquot pedunculis longis gracilibus rhachibusque curtissimis. *Flores* congesti globos facientes. *Legumina* plana oblonga acuminata.

Trees; branchlets terete, glabrous. *Leaves* with 6 or less pairs of leaflets; leaflets small, narrow, glabrous; rhachis winged; glands patelliform. *Inflorescences* 1-few, with long slender peduncles; rhachis very short. *Flowers* congested, giving a globose appearance; bracts linear, persistent; calyx irregular, cleft on one side, forming a well marked pointed projection. *Legume* flat, oblong, glabrous, acuminate.

Type species: *I. acuminata* Benth.

This series has affinities to the series DENSIFLORAE through *I. tenuipedunculata,* and to some DYSANTHAE (*I. ciliata* and *I. psitacorum*). It is confined to South America, and is formed by few, isolated species. In the area under study only one occurs. SPECIES . . . 29

29. INGA ACUMINATA Benth. in Hook., Lond. Jour. Bot. **4:** 600, 1845. (Type *Lockhart* 334)

Feuilleea acuminata (Benth.) O. Ktze., Rev. Gen. Pl. **1:** 187, 1891.

Trees up to 12 m tall; branchlets terete, glabrous, striate, sparsely lenticellate. *Leaves* with 2-4 pairs of leaflets; leaflets coriaceous, narrowly elliptic to lanceolate, often asymmetric, acute to long-acuminate at the apex, the base cuneate, above deep green, glabrous and lustrous, the nerves slightly prominent, beneath paler, punctate, glabrous, the nerves conspicuous, the upper pair 7-12 cm long, 3-4 cm wide, the lower pair 4-5 cm long, 2-3 cm wide; rhachis winged, 2-6 cm long, glabrous, the wings cuneate, up to 1.5 cm wide, the glands sessile, patelliform; petiole winged, 1.0-1.5 cm long, glabrous, the pulvinus terete and thick, about ¼ the total length; stipules ovate, 3-7 mm long, striate, pilose outside, semipersistent. *Inflorescences* solitary, axillary; peduncle slender, 3-7 cm long, striate, pilose; rhachis very short, 0.5-1.0 cm long, giving to the inflorescences a striking umbelliform appearance, the bracts linear-elliptic, 3-9 mm long, pilose, persistent. *Flowers* sessile, or shortly pedicellate; calyx tubular, ungulate at the apex in bud, about half cleft on one side, 9 mm long, sparsely pilose to glabrescent, the teeth obsolete; corolla tubular-funnelform, 11-12 mm long, densely strigose, the lobes

acute, about 2.5 mm long; staminal tube included or very slightly exserted, the filaments 1-2 cm long; ovary flat, glabrous, the style 3 cm long. *Legume* flat, oblong, slightly curved, shortly acuminate at the apex, the base rounded, 9-21 cm long, 2.0-2.5 cm wide, transversely striate, glabrous, the margins slightly elevated; seeds 18-20.

Trinidad. (Lowlands of northern South America, from Peru to Venezuela.)

TRINIDAD: Tabaguite, *Britton, Freeman & Nowell 2575* (GH); without locality, *Bot. Gard. Trin. Herb. 1043* (US), *Chicago Nat. Hist. Mus. Herb. 573834* (F), *Hart s. n.* (US), *Lockhart 334* (K).

A rare species (illustrated in Hooker, Ic. Pl. **13:** *t. 1202,* 1817) noteworthy especially for its calyx, which in bud has a long and curved acumen and which, once open, is perhaps the most irregular in the genus; also striking are the long-acuminate leaves and the congested inflorescence. Its closest ally is *I. urabensis* L. Uribe, of northern Colombia. Another species similar in foliar characters to *I. acuminata* is the little known *I. angustifolia* Willd. of Venezuela.

Series 6. **PILOSULAE** J. León, ser. nov.

Arbor mediocris; ramuli pilosi glabrescentesve. *Folia* maga foliolorum paribus paucis sparse flavo-pilosorum; rhachis alata. *Inflorescentiae* pedunculis curtis crassis; calyx confertim flavo-pilosus. *Legumina* plana tomento crasso flavo.

Medium sized *trees;* branchlets pilose to glabrescent. *Leaves* large, with few pairs of leaflets, thin or chartaceous, sparsely yellow-pilose; rhachis winged, the glands thin and stipitate. *Inflorescences* with short, stout peduncles; the flowers congested in a very short rhachis; calyx tubular, deeply cleft, striate, sparsely pilose; corolla tubular, densely yellow-pilose. *Legume* flat, oblong, covered with a yellow, thick tomentum.

Type species: *I. pilosula* (Rich.) Macbride

The PILOSULAE are characterized by large leaves, short peduncles in which the flowers form a congested inflorescence, and densely yellow-pilose legumes. They seem to be intermediate between the previous series and some of the large flowered species of *Inga* such as in the VULPINAE.

A South American group with marginal representatives in Trinidad and Central America. SPECIES . . . 30-32

a. Leaves with 2 pairs of leaflets; leaflets long-acuminate, peduncle 4-10 cm long. Trinidad .... 30. I. PILOSULA
aa. Leaves with more than 2 pairs of leaflets; leaflets obtuse or acute at the apex; peduncle 1-4 cm long.
  b. Upper leaflets oblong to obovate; peduncle less than 1.5 cm long; corolla 12-16 mm long. Panama........ 31. I. HAYESII
  bb. Upper leaflets elliptic-oblong; peduncle 2-4 cm long; corolla 18-22 mm long. Costa Rica .... 32. I. VENUSTA

30. INGA PILOSULA (Rich.) Macbride, Publ. Field Mus. Nat. Hist., Bot. Ser., **13:** 41, 1943.

Mimosa pilosula Rich., Act. Soc Hist. Nat. Paris **1:** 113, 1792 (Type *Le Blond s.n.* photo)
Inga quassiaefolia Willd. in L., Sp. Pl. **4:** 1013, 1806. (Type *Hoffmansegg s.n.* photo)

I. nitida Willd., loc. cit. (Type *Hoffmansegg s.n.* photo)
Mimosa lucida Vahl, Eclog. **3:** 31, 1807. (ex char.)
M. quassiaefolia (Willd.) Poir. in Lam., Encycl. Suppl. **1:** 41, 1810.
M. nitida (Willd.) Poir., loc. cit.
Inga pilosiuscula (Rich.) Desv., Jour. Bot. **1:** 71, 1816.
I. setifera DC., Prodr. **2:** 432, 1825. (Type *Mus. Paris s.n.* photo)
I. platycarpa Benth. in Hook., Lond. Jour. Bot. **2:** 142, 1840 (*fide* Bentham). (Type *Schomburgk 534,* not seen)
I. affinis Steud., Flora **1843:** 758, 1843. (Type *Hostmann & Kappler 1157*)
Feuilleea pilosula (Rich.) O. Ktze., Rev. Gen. Pl. **1:** 186, 1891.
F. quassiaefolia (Willd.) O. Ktze., loc. cit.
F. setifera (DC.) O. Ktze., loc. cit.

Trees 6 to 14 m tall; branchlets terete, striate, dense ferrugineous-pilose or glabrous, lenticellate. *Leaves* large, with 2 pairs of leaflets; leaflets coriaceous to chartaceous, broadly elliptic, asymmetric, the apex markedly acuminate, the acumen about 1 cm long, the base acute to obtuse, oblique, above dark and lustrous, sparsely pilose to glabrous, the nerves impressed, beneath paler, more densely pilose to glabrous, the nerves prominent, the upper pair broadly elliptic, cuneate at the lower half, 14-19 cm long, 7-9 cm wide, the basal pair elliptic-ovate, 9-10 cm long, 6-7 cm wide; rhachis broadly winged, pilose to glabrous, 4-8 cm long, the wings cuneate, the glands crateriform, about 2 mm in diam, glabrous, the apical appendix linear, 4-10 mm long, pilose, caducous; petiole winged above, 0.5-5.5 cm long, pilose to glabrescent, the pulvinus about 1 cm long, thick and darker; stipules linear, 4-10 mm long, pilose, deciduous. *Inflorescences* axillary, 1-2 spikes in each axil; peduncle terete, 4-10 cm long, striate, ferrugineous-pubescent to glabrous; rhachis 1-2 cm long, the bracts linear, 4 mm long, pilose, caducous. *Flowers* sessile, yellow, congested; calyx tubular, cleft on one side, 6-7 mm long, pilose, striate; corolla tubular-funnelform, 12-16 mm long, appressed-pilose, the hairs bright yellow, the lobes acute, 1.5-2.0 mm long; staminal tube included to slightly exserted, the filaments up to 2.5 cm long. *Legume* flat, thin, oblong, 8-17 cm long, 3-4 cm wide, transversely striate, in age glabrate, the margins elevated.

Lowland forests of Trinidad. (Amazonian Peru and Brazil, Venezuela and the Guianas.)

TRINIDAD: Maravaltful, O. *Kuntze 792* (F, US); O'Meara savanna, *Britton & Britton 2507* (US); Providencia, Sta. Cruz, *Broadway 6591* (MO); San Jose, O. *Kuntze 864* (F); Via Valencia, *Broadway 2292* (F, GH, MO, US); WITHOUT LOCALITY, *Trin. Bot. Gard. Herb. 2845* (F).

Inga pilosula has attracted the attention of travelers and botanists by its yellow flowers, so unusual in this genus. Its variability is evidenced by the abundant synonymy in which specific epithets referring to the indument are so common as to indicate that the variability is largely to be found in the indument rather than in more stable characters. Some of the Trinidad specimens are glabrous, while the majority of the Venezuelan and Guianan plants are densely pilose. The names *I. nitida* and *I. quassiaefolia* have been used for the Brazilian specimens with glabrous and lustrous leaves. It may be possible that these names represent different species, but at present no important morphological characters seem to permit a separation of species in the material examined.

31. Inga hayesii Benth., Trans. Linn. Soc. **30:** 617, 1875. (Type *Hayes* 62)

Small *trees,* 3 to 9 m tall; branchlets terete, pilose when young, in age glabrate, lenticellate. *Leaves* with 2-4 pairs of leaflets; leaflets oblong to obovate, the base rounded to acute, often asymmetric, above strigose or sparsely pilose, the nerves prominent or in shallow grooves, beneath densely pilose, the nerves prominent, the upper pair oblong-elliptic to obovate, generally very asymmetric, 7-14 cm long, 3-6 cm wide, the lowermost pair obliquely ovate to elliptic, 4-6 cm long, 2-3 cm wide; rhachis winged, 3-9 cm long, strigose especially along the midnerve, ending in a linear apex (sometimes a terminal leaflet), the wings cuneate, up to 1 cm wide, the glands shortly stipitate, about 1 mm in diam, concave and glabrous at the apex; petiole terete at the pulvinar section, winged or marginate above, 1-2 cm long, pilose; stipules obovate, acute, up to 6 mm long, tomentose without, semipersistent. *Inflorescences* axillary, solitary or clustered, sessile or shortly pedunculate; peduncles terete, up to 1.5 cm long, ferrugineous-strigose; rhachis strigose, 1.5-2.5 cm long, the bracts oblong, about 2 mm long, acute, pubescent outside, caducous. *Flowers* sessile, congested; calyx tubular, generally deeply cleft on one side, 6-11 mm long, dark reddish, striate, pilose at the base, glabrescent, the teeth small, irregular, 1-2 mm long, with tufts of hairs at the tips; corolla tubular-funnelform, 12-16 mm long, densely strigose, the lobes acute, 2-4 mm long; staminal tube included, the filaments up to 3 cm long. *Legume* flat, thick in age, 10 cm long, 1.5 cm wide in a young specimen, densely yellow-strigose.

Lowlands of Panama. (Colombia.)

Panama: canal zone: Balboa, *Correll 12273* (GH); Chivi-Chivi trail, *Maxon & Harvey 6608* (US); Fort Kobe, *Allen 1890* (GH, MO, NY, US); Cocoli, *Riley 122* (US); Miraflores, *P. White 79* (GH, MO, NY); Paraíso, *Hayes 62* (K). panama: Bella Vista, Panama City, *Maxon & Valentine 6931* (F, GH, US), *6946* (F); Matías Hernández, *Pittier 6714* (F, GH, NY, US); Monte Oscuro, *Zetek 3497* (F); Old Panama, *Riley 140* (US); Pacora, *Woodson, Allen & Seibert 759* (MO, NY, US); Panamá, *Sargent 25* in part (US); Pedro González, Perlas Islands, *Allen 2593* (MO).

In *I. hayesii,* as in the Costa Rican *I. venusta,* there is a marked trend towards a short, almost obsolete peduncle accompanied by a reduction of the floral rhachis, which gives a capitate and often sessile appearance to the inflorescences; the calyx is noteworthy also for the reddish color and deeply cleft sides.

32. Inga venusta Standley, Publ. Field Mus. Nat. Hist., Bot. Ser., **18:** 500, 1937. (Type *Brenes 6256*)

Trees; branchlets terete, glabrous, densely lenticellate. *Leaves* with 3-4 pairs of leaflets; leaflets coriaceous oblong to lanceolate, asymmetric, obtuse to obtusely acuminate at the apex, the acumen up to 1 cm long, the base obtuse to rounded, above lustrous, glabrous, the nerves slightly impressed, beneath glabrous, the main nerves and reticulate enervation conspicuous, the upper pair elliptic, generally very oblique, 10-18 cm long, 3-4 cm wide, the lower pairs elliptic to lanceolate, 4-13 cm long, 2.0-4.5 cm wide, the petiolules dark, about 1 mm long, pilose; rhachis cuneately winged, 3.5-11.0 cm long, sparsely pilose on the midnerve,

the wings up to 1.5 cm wide, glabrous, the glands stipitate, pertuse at the apex, about 1 mm in diam, the appendix linear, about 12 mm long; petiole winged above, 1.5-6.0 cm long, sparsely pilose to glabrous, the pulvinus terete, about 0.5 cm long. *Inflorescences* axillary or in groups in the terminal branchlets, solitary or 2-3 in each axil; peduncle terete 2.0-2.5 cm long, striate, sparsely pilose; rhachis 0.5-1.0 cm long, the bracts less than 1 mm long, caducous. *Flowers* sessile, congested; calyx cupulate-tubular, deeply cleft on one side, 6-9 mm long, above glabrous and striate, pilose at the base, the teeth very small and irregular; corolla tubular, 18-22 mm long, with a dense, yellow pubescence, the lobes 4 mm long; staminal tube included, the filaments about 1.5 cm long; ovary glabrous. *Legume* unknown.

Wet forests of central Costa Rica.

Vernacular name: *guabo amarillo* (Costa Rica—Brenes).

COSTA RICA: ALAJUELA: La Palma, San Ramón, *Brenes 6255* (CR, F, IAIAS), *Brenes 6256* (CR, F, IAIAS).

An endemic and poorly known species; its closest relationship seems to be with *I. hayesii* of the lowlands of Panama. Both have the same type of inflorescence, a short spike with congested rhachis, and similar structure in the deeply cleft calyx. *Inga venusta* differs in the glabrous and more lanceolate leaves.

Series 7. CALOCEPHALAE Benth. in Hook., Lond. Jour. Bot **4:** 609, 1845.

Trees; branchlets angulate or terete, densely yellow-hispid when young, glabrate in age. Leaflets large, densely pilose; rhachis winged; stipules large ovate to lanceolate, subpersistent. *Inflorescence* long pedunculate, the bracts well developed, subpersistent. *Flowers* large, sessile; calyx tubular, narrow, more than 15 mm long, glabrescent; corolla tubular, 30-45 mm long, hirsute. *Legume* flat, 25-35 cm long, 4-6 cm wide, densely yellow-pilose.

Series CALOCEPHALAE is here restricted to a group of species centering around *I. fastuosa* Willd. and *I. macrophylla* Willd., of which only two representatives are found in the area under study, *I. mucuna* Walp. & Duchass. from Panama, and *I. venosa* Benth. from Trinidad.

Bentham and Pittier placed in the CALOCEPHALAE several species that in the present treatment are put in different series. They were maintained in the same group with the species mentioned above on the basis that all them have large and subpersistent stipules and bracts, although they are quite distinct in flower and fruit characters. SPECIES . . . 33-34

a. Stipules ovate, 7-8 mm long; bracts 5-9 mm long; branchlets tomentose; petiole terete or marginate. Panama .... 33. I. MUCUNA
aa. Stipules lanceolate, about 16 mm long; bracts 10-15 mm long; branchlets long-pilose; petiole winged. Trinidad .... 34. I. VENOSA

33. INGA MUCUNA Walp. & Duchass. in Walp., Ann. Bot **2:** 456, 1851-52. (Type *Duchassaing 81*)

Trees up to 20 m tall; branchlets terete or angulate, densely ferrugineous-pubescent. *Leaves* with 3-4 pairs of leaflets; leaflets ovate, the apex acute to acumi-

nate, the base rounded, sometimes asymmetric, above sparsely pilose, the costa and main nerves prominent and more pubescent, beneath densely pilose, the hairs yellow and curved, the nerves prominent, the upper pair ovate to elliptic-ovate, 13-19 cm long, 7-11 cm wide, the basal pair ovate, 6-12 cm long, 4-5 cm wide; the petiolule short, conic, 2-3 mm long, densely pubescent; rhachis winged, 11-14 cm long, densely tomentose along the midnerve, the wings cuneate, each about 5 mm wide, sparsely pilose, the glands small, umbiliciform, less than 1 mm in diam, glabrous; petiole terete or slightly winged, 1.5-3.5 cm long, densely ferrugineous-pilose, the pulvinus thicker; stipules ovate, 7-8 mm long, 5-8 mm wide, minutely pubescent, apiculate, deciduous. *Inflorescences* solitary or in groups, axillary, long pedunculate; peduncle terete, 4-7 cm long, densely ferrugineous-tomentose; rhachis 3.0-4.5 cm long, the bracts triangular, 5-9 mm long, yellow-pubescent, subpersistent. *Flowers* numerous, sessile; calyx tubular, 17-20 mm long, striate, glabrous except at the tip, the teeth small, acute, about 1 mm long, sericeous; corolla tubular, 40-55 mm long, sparsely sericeous; the lobes acute, slightly spreading, 5 mm long; staminal tube exserted, the filaments up to 4 cm long. *Legume* flat, straight or twisted, 25-33 cm long, 5-6 cm wide, 0.5 cm thick, densely ferrugineous-hirsute, the margins rounded.

Lowlands of Panama.

PANAMA: CANAL ZONE: Balboa, *Standley 27172* (NY, US), *32124* (US); Barro Colorado Island, *Woodworth & Vestal 665* (F). DARIEN: Boca de Cupé, *Allen 882* (MO, NY, US); Sambú River, *Pittier 5525* (NY, US). PANAMA: Panamá, *Duchassaing 81* (GH), *Sargent 25* in part (US).

Inga mucuna is the only Central American representative of the series CALOCEPHALAE. Its closest allies are *I. fastuosa* of Venezuela and *I. venosa* endemic to Trinidad. Further collections may prove the independence of the three species or their grouping into one unit.

34. INGA VENOSA Griseb. ex Benth., Trans. Linn. Soc. **30:** 623, 1875. (Type *Sieber distr. Wabra 104*)

Trees 10 to 15 m tall; branchlets terete, striate, densely ferrugineous-hirsute, lenticellate. *Leaves* with 3-4 pairs of leaflets; leaflets elliptic to ovate, subchartaceous, the apex acute, obtuse to markedly acuminate, the acumen 3-4 mm long, pilose, the base rounded, unequal, above lustrous, sparsely pilose to glabrescent, the nerves impressed, beneath dull, more densely pilose, the nerves prominent, the upper pair broadly elliptic, 15-22 cm long, 7-9 cm wide, the basal pair ovate, 6-9 cm long, 4-6 cm wide, the petiolule about 2 mm long, densely pilose; rhachis winged, 9-17 cm long, ending in a linear appendix, 12 mm long, pilose, the wings cuneate, each up to 1 cm broad, pilose, the glands stipitate, glabrous and patelliform at the apex; petiole winged, 2.0-2.5 cm long, pilose, the pulvinus about 0.5 cm long, densely ferrugineous-pilose; stipules triangular, long-acuminate, 14-17 mm long, densely pilose to glabrescent, persistent. *Inflorescences* axillary, in groups, peduncle and rhachis ferrugineous-pubescent, the bracts lanceolate, 10-15 mm long, pilose. *Flowers* sessile; calyx tubular, 15-22 mm long, striate, glabrescent, the teeth

acute, 2-3 mm long, pilose at the tips; corolla tubular-funnelform, 32-42 mm long, appressed-pilose to glabrescent, the lobes acute, 4 mm long, densely pilose; staminal tube exserted. *Legume* (*fide* R. O. Williams) flat, oblong, up to 28 cm long, 4 cm wide, densely ferrugineous-hirsute, the margins elevated.

Lowland forests of Trinidad.

TRINIDAD: Talparo, *Britton, Britton & Freeman 2164* (GH); WITHOUT LOCALITY, *Sieber distr. Wabra 104* (GH, MO).

Inga venosa belongs to a group of South American species that centers around *I. macrophylla;* it differs from the rest of them in the slender flowers and in this character is closer to the endemic Panamanian *I. mucuna.* It also has been confused with the Venezuelan *I. fastuosa* Willd., which has broader flowers, although in leaves and fruits they seem to be quite similar. This is the only endemic species of *Inga* in Trinidad.

Series 8. **GOLDMANIANAE** J. León, ser. nov.

Arbor; ramuli angulati vel teretes. *Folia* magna pilosa; rhachis alata. *Inflorescentiae* pedunculis longis. *Flores* sessiles in alabastro globosi; calyx praesertim magnus dense flavo-pilosus; corolla confertim albosericeus. *Legumina* plana flavo-hirsuta.

Trees; branchlets angulate to terete, densely yellow-pilose, or glabrate. *Leaves* large, pilose, with supernumerary glands on the costa of the leaflets; rhachis winged. *Inflorescences* long-pedunculate, the bracts 5-6 mm long, caducous. *Flowers* sessile, spheric in bud; calyx unusually large, 12-17 mm long, 8-12 mm wide, densely yellow-pilose; corolla 25-28 mm long, 10-15 mm wide, densely white-sericeous. *Legume* flat, 20-25 cm long, 4-6 cm wide, yellow-hirsute.

Type species: *I. goldmanii* Pittier.

The only representative of this series is *I. goldmanii* Pittier from Costa Rica and Panama. The most striking character is the flower, which in size could be compared only with that of *I. sessilis* Benth. of southern Brazil. *Inga goldmanii* does not seem to have any close ally among the species of *Inga* that I have studied from Central and South America. SPECIES . . . 35

35. INGA GOLDMANII Pittier, Contr. U. S. Nat. Herb. **18:** 198, 1916.—Fig 4. (Type *Goldman 1866*)

Large *trees* up to 20 m tall; branchlets terete, striate, densely ferrugineous-hirsute, sparsely lenticellate. *Leaves* with 3-5 (generally 4) pairs of leaflets; leaflets elliptic to ovate, acute to acuminate at the apex, the acumen linear, up to 6 mm long, the base cordate to rounded, generally asymmetric, above lustrous, sparsely pilose to glabrous, the costa and lateral nerves impressed and more pubescent, the former with a gland at less than 2 cm from the rhachis, beneath pilose, scabrous, the nerves prominent and more pilose, the upper pair elliptic, 18-25 cm long, 7-14 cm wide, the intermediate pairs ovate to elliptic-ovate, 9-15 cm long, 5-8 cm wide, the lowermost pair ovate, 5-9 cm long, 3-6 cm wide, the peti-

olules short, conic, 2 mm long, pubescent to glabrous; rhachis winged, 14-25 cm long, densely hirsute, the wings broader in the upper interfoliolar sections, elliptic, each side up to 11 mm wide, sparsely pilose, the terminal appendage linear, 6-9 mm long, tomentose, the glands long and slenderly pedicellate, 4 mm long, glabrous; petiole winged above, 1.5-4.0 cm long, ferrugineous-hirsute, the pulvinar section thicker and terete; stipules cordate, obtuse, up to 12 mm long and 20 mm wide, pilose, deciduous. *Inflorescences* axillary, generally solitary; peduncle stout, 4-8 cm long, densely ferrugineous-hirsute; rhachis 4-7 cm long, the bracts cordate, 6 mm long, densely tomentose, caducous. *Flowers* unusually large, sessile, distant, spherical in bud; calyx campanulate, 12-17 mm long, 8-12 mm wide, densely yellow-pilose, the teeth obtuse, 4-6 mm long; corolla tubular-campanulate, 25-28 mm long, 10-15 mm wide, densely white-sericeous; staminal tube included, the filaments up to 45 mm long. *Legume* flat, oblong, straight or curved, twisting in age, up to 25 cm long, 6 cm wide, 1 cm thick, densely ferrugineous-hirsute, the margins rounded.

Rain forests of the Atlantic watershed in Costa Rica and Panama.

COSTA RICA: ALAJUELA: Los Chiles, *Holm & Iltis 951* (MO). LIMON: Banana River near Limón, *Cook & Doyle 429* (US); Limón, *Lankester 172* (K); Livingston on the Reventazón River, *Rowlee & Stork 788* (NY, US); Río Hondo, *Pittier 16376* (CR, US); Shirores, Talamanca, *Tonduz 9358* (CR, US).

PANAMA: BOCAS DEL TORO: Cricamola, Almirante, *G. P. Cooper 527* (F). CANAL ZONE: Barro Colorado Island, *Avilés 68* (F), *Bailey & Bailey 223* (F), *Bangham 392* (F), *396* (F), *Killip 40021* (MO, US), *Shattuck 514* (F), *584* (F), *Standley 40999* (US), *Starry 231* (F), *Wetmore & Abbe 15* (F, GH), *15a* (F), *Woodworth & Vestal 321* (F), *Zetek 3461* (F), *3462* (F); Frijoles, *Allen 922* (GH, MO); Gatún, *Goldman 1866* (US); Lion Hill Station, *Hayes 598* (US); Monkey Hill, *Lehmann 1001* (US); Salamanca, *Steyermark & Allen 16754* (GH); without locality, *Epplesheimer s. n.* (F).

This species, without any apparent affinity, is one of the most striking *Leguminosae* of Central America. It grows in the rain forest where it attains the level of the highest trees. Especially noteworthy are the large flowers surpassed in size in this genus only by *I. sessilis* Benth. of southern Brazil. Another rare character is the foliolar glands, more conspicuous in the seedlings and young leaflets, paralleled only in *I. adenophylla* Pittier and *I. pruriens Poepp.*, both of the upper Amazon.

Series 9. DYSANTHAE Benth., Trans. Linn. Soc. **30:** 625, 1875.

Trees; branchlets terete, ferrugineous-pilose. *Leaves* large; leaflets glabrous and sublustrous above, densely and softly pilose beneath; rhachis terete (generally winged in the South American species). *Inflorescence* pedunculate, the bracts small, caducous. *Flowers* distant; calyx cupular-shaped, 4-5 mm long, lanose; corolla up to 18 mm long, lanose, pinkish. *Legume* flat, densely pilose.

SPECIES . . . 36

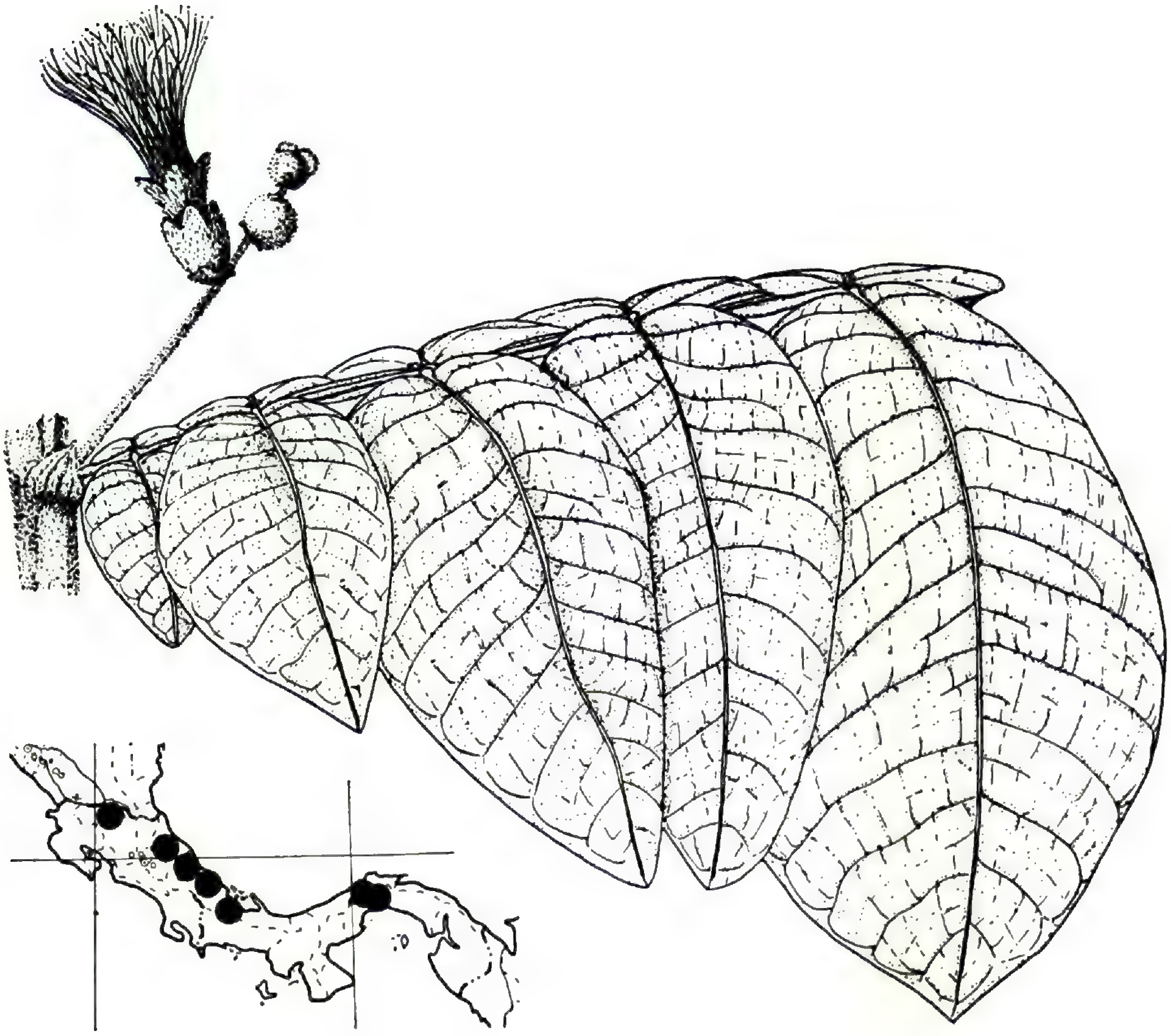


Fig. 4. *Inga goldmanii* Pittier

36. Inga standleyana Pittier, Contr. U. S. Nat. Herb. **18:** 204, 1916. (Type *Pittier 5496*)

Low *trees;* branchlets terete, densely ferrugineous-pilose. *Leaves* with 4 pairs of leaflets; leaflets obovate to elliptic, subchartaceous, the apex obtuse to markedly apiculate, the base obtuse to rounded or subemarginate, above opaque, sparsely pilose to glabrescent, closely pilose on the depressed nerves and margins, beneath paler, densely yellow-pilose, the 11-14 lateral nerves very prominent, the reticulate nervation conspicuous, the upper pair rhombic-ovate to elliptic, oblique and cuneate at the base, 11.0-13.5 cm long, 7.5-8.0 cm wide, the lower pair elliptic to ovate, 6-7 cm long, 4.0-4.5 cm wide, the petiolules conic, about 1.5 mm long, densely pilose; rhachis terete, 3.0-3.5 cm long, ferrugineous-pubescent; stipules triangular, 2 mm long, pilose, caducous. *Inflorescences* axillary or terminal, solitary or paired; peduncle terete, 1.5-4.0 cm long, striate, ferrugineous pilose; rhachis 4.5-6.0 cm long, the bracts ovate, caducous. *Flowers* distant, sessile, soon deciduous; calyx cupular-shaped, 4-5 mm long, densely lanose, the teeth shallow, about 1 mm long, corolla broad, funnelform, 15-18 mm long, lanose, the lobes broad, obtuse, 3-4 mm long; staminal tube included to slightly exserted, pinkish, the

filaments about 2.5 cm long; ovary lanose. *Legume* (*fide* Pittier) flat, densely ferrugineous-pilose.

Rain-forests of western Panama.

PANAMA: DARIEN: vic of La Palma, *Pittier 5496* (GH, US).

An endemic species regarded by some authors as close to *I. dysantha* Benth. (Type *Spruce 1816*) but easy to separate because of its unwinged rhachis and the size of its flowers. The closest ally, however, is *I. rubiginosa* DC. placed by Bentham and Pittier in EUINGA-SULCATAE, probably on the slight similarity in foliage characters. *Inga rubiginosa* is quite a variable species; it has, like *I. standleyana*, a terete rhachis and a very similar type of leaves. The flowers are larger and more slender than in the Panamanian plants. *Inga standleyana* is the only member of the series DYSANTHAE in North America.

Series 10. **SPECTABILES** J. León, ser. nov.

Arbor; ramuli angulati, glabrescens. *Folia* magna, glabrescens; rhachis teretia vel alata. *Inflorescentiae* pedunculis brevis, bracteis magnis. *Flores* sessiles congesti. *Legumina* plana, glabrata.

Large *trees;* branchlets angulate, glabrescent. *Leaves* large; leaflets chartaceous, glabrous or sparsely pilose; rhachis terete, subalate or winged; stipules linear-lanceolate, 6-9 mm long, subpersistent. *Inflorescences* shortly pedunculate; bracts large, tomentose, subpersistent. *Flowers* sessile, clustered; calyx cleft to one side, 8-9 mm long, densely pubescent; corolla tubular, 18-24 mm long, tomentose. *Legume* flat, 30-70 cm long, 4-8 cm wide, glabrous.

Type species: *I. spectabilis* (Vahl) Willd.

This series corresponds to SPECTABILES, rank unspecified, Britton & Killip, Ann. N.Y. Acad. Sci. **35:** 111, 1936, a nomen nudum, and in part to SPECTABILES, Gutiérrez, Rev. Fac. Nac. Agr. Col. **7:** 53, 1947, also a nomen nudum.

Inga spectabilis Willd. is the only member of this series that occurs in Central America. Several other species have been described from northern South America.

SPECIES . . . 37

37. INGA SPECTABILIS (Vahl) Willd. in L., Sp. Pl. **4:** 1017, 1806. (ex char.)

Mimosa spectabilis Vahl, Skr. Nat. Selsk. Kjob. **21:** 219, *pl. 10,* 1792.
Inga fulgens Kunth, Mim. 36, *pl. 11,* 1819. (ex char.)
I. lucida H.B.K., Nov. Gen. Sp. Pl. **6:** 287, 1824. (ex char.)
Feuilleea spectabilis (Vahl) O. Ktze., Rev. Gen. Pl. **1:** 184, 1891.
Inga smithii Britton ex Britton & Killip, Ann. N. Y. Acad. Sci. **35:** 117, 1936. (Type *Killip & Smith 14923*)

Trees up to 12 m tall, the crown spreading; branchlets angulate, glabrescent, lenticellate. *Leaves* large, with 2-3 pairs of leaflets; leaflets elliptic to obovate, coriaceous, the apex rounded to mucronate, the base asymmetric, obtuse to cordate, above dark green, lustrous and glabrescent, the nerves deeply impressed and sparsely pilose, beneath paler, sparsely pilose, the nerves very prominent, more densely pilose, the upper pair 19-28 cm long, 8-15 cm wide, the basal pair 10-16 cm long, 5-9 cm wide, the petiolules conic, 3-5 mm long, pilose; rhachis terete to winged, up to 11 cm long, pubescent or lenticellate, the wings cuneate, broader above, each obsolete to 12 mm wide, the glands short, patelliform, 2-3 mm in

diam; petiole stout, subterete, sometimes winged above, 6-15 mm long, puberulent; stipules linear to lanceolate, acute, 6-9 mm long, about 4 mm wide, subpersistent. *Inflorescences* 2-6 in terminal panicles, or solitary and axillary; peduncles angulate, 3-8 cm long, striate, puberulent; rhachis 1-5 cm long, the lower bracts cordate, 8-14 mm long, 6-11 mm wide, tomentose and subpersistent, the upper bracts elliptic, 8-10 mm long, 3-5 mm wide, densely tomentose. *Flowers* congested, sessile; calyx tubular, cleft to one side, 8-9 mm long, densely pubescent, the teeth spreading, about 3 mm long; corolla tubular, 18-24 mm long, tomentose, the lobes spreading; staminal tube slightly exserted, the filaments up to 4 cm long. *Legume* flat, oblong, woody, straight or slightly curved, up to 70 cm long, 8 cm wide and 3 cm thick, glabrous, the margins not elevated; seeds numerous, surrounded by scanty aril.

Mexico; southern Central America. (Colombia and Venezuela).

Vernacular names: *guabo machete* (Costa Rica); *guabo real* (Panama).

MEXICO: OAXACA: Ubero, *Ll. Williams 9277* (F), *9386* (F).

COSTA RICA: ALAJUELA: Guatuso, *Holm & Iltis 834* (MO); Muelle de San Carlos, *León 2426* (IAIAS). PUNTARENAS: Boruca, *Tonduz 4765* (CR); Buenos Aires, *Tonduz 3826* (CR). SAN JOSE: El General, *Skutch 2727* (GH, MO, NY, US).

PANAMA: BARU: Progreso, *Cooper & Slater 203* (F, NY, US). BOCAS DEL TORO: Changuinola Valley, *Cooper & Slater 124* (US); Fish Creek, *von Wedel 2392* (GH, US). CANAL ZONE: Ancón, *Maxon s. n.* (US); Balboa, *Standley 29243* (US); Barro Colorado Island, *Avilés 925* (F), *Bailey & Bailey 293* (F), *409* (F), *Kenoyer 370* (US), *Zetek 3481* (F), *3489* (F), *3669* (F); Culebra, *Pittier 2423* (GH, NY, US); Las Cascadas, *Pittier 3476* (US). CHIRIQUI: San Félix to Cerro Flor, *Allen 1944* (GH, MO, US). COCLE: Bismarck, Penonomé, *R. S. Williams 383* (NY), *584* (NY). PANAMA: Juan Díaz, *Standley 30571* (US); Las Sabanas, *Bro. Paul 139* (US); Río Tapia, *Standley 28147* (US); Taboga Island, *Maxon 6922* (GH, US). WITHOUT LOCALITY: *Kuntze 1923* (NY).

Inga spectabilis is a striking tree when loaded with the long, pendant fruits. It is planted commonly around the Indian dwellings for its fruits and as a shade tree in the pastures of the lowlands. The specimens examined, as well as many from Colombia and Venezuela, show rather restricted variability. *Inga smithii* is based on a young specimen more densely pubescent than the adult plants. The Mexican specimens, known only in fruit, show a remarkable discontinuity and, although their foliage and legumes are similar to the southern plants, only more collections will prove the correctness of this relationship.

An incomplete specimen from Guatemala, *Pittier 1911: 200*, also may belong to this species.

Series 11. VULPINAE Benth. in Hook., Lond. Jour. Bot. **4**: 604, 1845.

Trees; branchlets angulate to terete, densely yellow-pilose when young, in age glabrate. *Leaves* large; folioles pilose, acuminate; rhachis winged, the glands slenderly pedicellate; stipules ovate, pilose, persistent. *Inflorescences* shortly pedunculate; bracts long, acute, persistent. *Flowers* sessile; calyx tubular, less than 5 mm wide, glabrescent; corolla tubular, densely pilose. *Legume* flat, thin, densely yellow-pilose.

This series is formed by few species, many of them restricted to the southern limit of the genus. Among them the most typical are *I. vulpina* Mart. and *I. hirsutissima* Rusby, the latter quite close to the Central American *I. tonduzii* J. D. Smith.

SPECIES . . . 38

38. Inga tonduzii J. D. Smith, Bot. Gaz. **44:** 112, 1907.—Fig 5. (Type *Tonduz 12928*)

Trees up to 12 m tall; branchlets terete, the young one aristate, hirsute. *Leaves* with 2, generally 3-4 pairs of leaflets; leaflets elliptic to cordate, the apex long-acuminate, the acumen filiform and densely pilose, the base acute to cordate, oblique, above densely yellow-pilose, especially on the costa and margin, or glabrescent and lustrous, the nerves impressed, beneath even and densely pilose, the nerves prominent, the upper pair elliptic to obvate, 11-16 cm long, 5-7 cm wide, the intermediate lanceolate, the basal pair cordate, 2.5-4.0 cm long, 1.5-2.0 cm wide, the petiolules less than 1 mm long, densely ferrugineous-pilose; rhachis winged, 2-9 cm long, closely pilose along the midrib, the wings elliptic, each about 4 mm wide, sparsely pilose, the acumen linear, up to 15 mm long, pilose, the glands clearly stipitate, 4 mm long, glabrous; petiole short, slightly winged, 1.0-1.5 cm long, pilose; stipules triangular, cordate, acuminate, 15-20 mm long, pubescent, persistent. *Inflorescences* axillary, solitary or 2-3; peduncle terete, 1-2 cm long, densely pilose; rhachis 1-4 cm long, the bracteoles lanceolate, 15-18 mm long, persistent. *Flowers* congested, sessile; calyx tubular, 10-16 mm long, striate, pilose to glabrescent, the teeth acute, 3-6 mm long, pilose; corolla tubular, deeply lobed, 20-27 mm long, yellow-sericeous, the lobes acute, 4-9 mm long; staminal tube included. *Legume* flat, oblong, apiculate, 15-30 cm long, 4-5 cm wide, 0.5 cm thick, densely fulvous-pilose to glabrous in age, the margins elevated.

Highlands of central Costa Rica, 600-1400 m elevation.

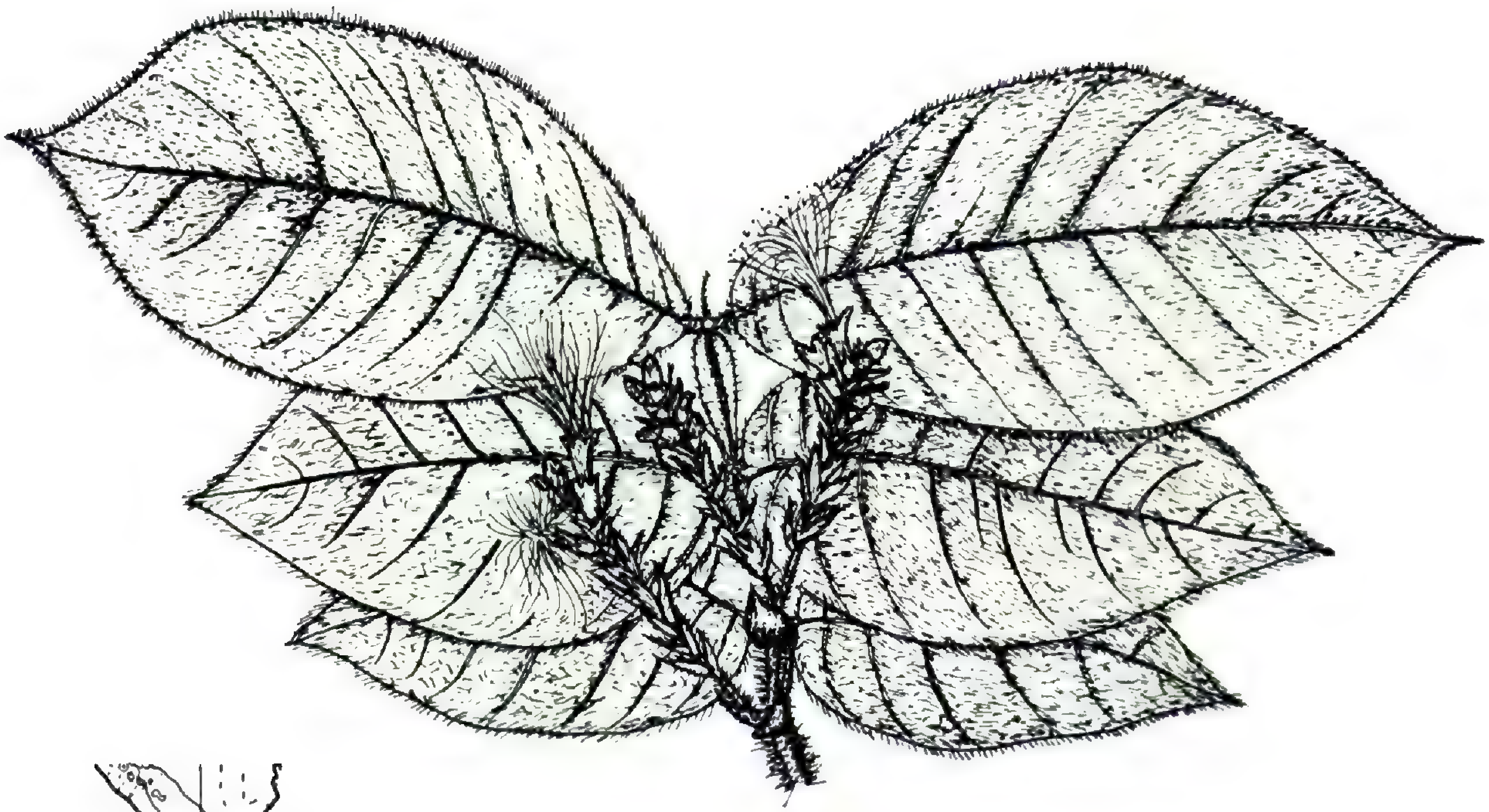
Vernacular name: *guabo amarillo, guabo peludo* (Costa Rica).

Costa Rica: alajuela: La Palma, San Ramón, *Brenes 6268* (CR, F), *6820* (CR, F), *17163* (CR, F); Zapote, San Carlos, *A. Smith 1307* (F, NY), *2655* (MO). cartago: Cartago, *Torres 98* (F); Las Vueltas, Tucurrique, *Tonduz 12928* (GH, US); Orosi, *Pittier s. n.* (NY); Turrialba, *Córdoba 34* (IAIAS), *97* (IAIAS), *León 3921* (MO, IAIAS). san jose: La Palma. *Standley 38076* (US).

Inga tonduzii is especially noteworthy for its short and pilose inflorescences congested in the axils of the leaves and its large pilose fruits. It is often seen in the coffee groves, among other common species, although its size and slow growth make it unsuitable as a shade tree.

Series 12. tetragonae Pittier, Contr. U. S. Nat. Herb. **18:** 205, 1916.

Trees; branchlets terete to angulate, sparsely pilose to glabrous. *Leaves* large, the folioles sparsely pubescent to almost glabrous; rhachis winged to marginate or terete, the glands small and cupuliform; stipules ovate, sparsely pilose, persistent. *Inflorescences* shortly pedunculate, the bracts persistent. *Flowers* sessile; calyx tubular, striate, shortly pilose; corolla tubular-funnelform, white-sericeous. *Legume* tetragonal, the margins as wide as the valves, ridged, the valves flat with prominent borders. species . . . 39



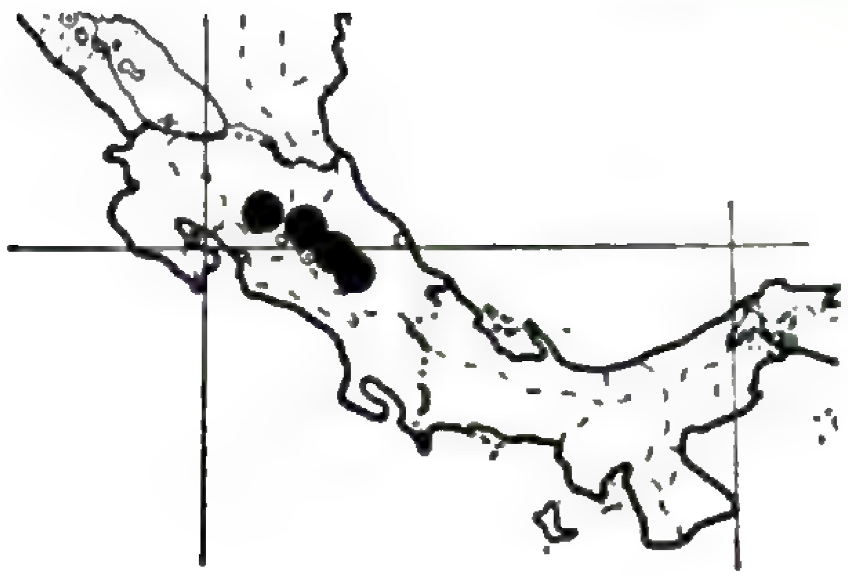


Fig. 5. *Inga tonduzii* J. D. Smith

39. Inga sapindoides Willd. in L., Sp. Pl. **4:** 1012, 1806. (Type *Bredemeyer s.n.*)

I. lindeniana Benth. in Hook., Lond. Jour. Bot. **4:** 608, 1845. (Type *Linden 726*)
I. panamensis Seem., Bot. Voy. Herald 117, 1853. (Type *Seemann 407*)
Feuilleea sapindoides (Willd.) O. Ktze., Rev. Gen. **1:** 189, 1891.
F. lindeniana (Benth.) O. Ktze., loc. cit. 188.
F. panamensis (Seem.) O. Ktze., loc cit.
Inga pittieri Micheli, Bull. Herb. Boiss. **2:** 466, 1894. (Type *Tonduz 4977*)
I. hartii Urb., Symb. Ant. **1:** 311, 1899. (Type *Hart 845*)
I. eggersii Harms in Engl., Bot. Jahrb. **42:** 88, 1908. (Type *Eggers 15075*)
I. preussii Harms in Fedde, Rep. Sp. Nov. **13:** 420, 1914 (Type *Preuss 1386* photo)
I. purpusii Pittier, Contr. U. S. Nat. Herb. **18:** 199, 1916. (Type *Purpus 6811*)
I. biolleyana Pittier, loc. cit. 207. (Type *Tonduz 8391*)
I. jimeneziana Pittier, loc. cit. 208. (Type *Tonduz 8333*)
I. rensoni Pittier, loc. cit. 209, 1916. (Type *Renson 239*)
I. rodrigueziana Pittier, loc. cit. (Type *Heyde & Lux 6095*)
I. salvadorensis Britton & Rose, N. Amer. Flora **23:** 12, 1928. (Type *Calderón 1828*)
I. caracasana Pittier, Trab. Mus. Com. Venez. 263, 1929. (Type *Pittier 9859*)
I. grandifolia Pittier, loc. cit. 264 (Type *Pittier 12621*)
I. camuriensis Pittier, loc. cit. 266 (Type *Pittier 13040*)
I. antioquensis Britton & Killip, Ann. N. Y. Acad. Sci. **35:** 118, 1936. (Type *Toro 858*)
I. chardonii Britton & Killip, loc. cit. 121. (Type *Chardon 135*)
I. panamensis Seem. var. *pittieri* (Micheli) Schery, Ann. Missouri Bot. Gard. **37:** 203, 1950.
I. panamensis Seem. var. *clavata* Schery, loc. cit. 204. (Type *von Wedel 672*)
I. panamensis Seem. var. *rodrigueziana* (Pittier) Schery, loc. cit. 205.
I. alotopetiola Schery, loc. cit. 206. (Type *Cooper & Slater 65*)

Trees 6 to 15 m tall; branchlets terete, on the new growth with a short and ferrugineous pubescence, in age glabrate and densely lenticellate. *Leaves* with 2-5 (generally 3-4) pairs of leaflets; leaflets chartaceous to membranaceous, broadly elliptic to lanceolate, the apex obtuse to acute, or shortly and abruptly acuminate, the base acute to rounded, often emarginate, above bright green, yellow-tomentose or scabrous to completely glabrous, the costa prominent and more pubescent, the lateral nerves ascending, slightly prominent to sunken, beneath paler, densely tomentose to glabrescent, the costa and lateral nerves prominent, the tertiary nervation transverse and conspicuous, the upper pair elliptic to obovate, strongly cuneate towards the base, often oblique, 9-20 cm long, 5-8 cm wide, the lower pair lanceolate, 5-12 cm long, 3-6 cm wide, the petiolules short and thick, 1-3 mm long, densely pilose; rhachis commonly winged only in the upper interfoliolar sections, or terete, 7-19 cm long, the wings elliptic or cuneate, the midrib prominent, densely pilose to glabrous, the glands obsolete to markedly pedicellate, crateriform to patelliform, 1-2 mm in diam, glabrous, with a wide and shallow pore, the terminal appendix linear-lanceolate, 5-8 mm long, pilose, caducous; petiole terete or marginate, 2-4 cm long, pubescent to glabrate; stipules ovate to lanceolate, up to 10 mm long, 8 mm wide, striate, densely pilose to glabrescent, persistent. *Inflorescences* 1-3, generally lateral from defoliated nodes and subtended by a pair of stipules, rarely terminal; peduncle terete, stout, 1-6 cm long, striate, pilose; rhachis 1-3 cm long, the bracts oblanceolate to spathulate, 8-15 mm long, striate, pilose; rhachis 1-3 cm long, the bracts oblanceolate to spathulate, 8-15 mm long, tomentose, persistent. *Flowers* sessile, distant or congested; calyx tubular, 9-17 mm long, striate, sparsely greenish-pilose to glabrate, the teeth acute to subulate, often irregular, 4-6 mm long, densely pilose; corolla tubular, dilating above, 18-30 mm long, appressed-pilose, the lobes 3-4 mm long; staminal tube included, the filaments about 4-5 cm long; ovary oblongoid, sulcate, the style 4-6 cm long, the stigma discoid. *Legume* tetragonal, 11-30 cm long, glabrous or sparsely pilose, the apex ending in a short and acute acumen, the base rounded, the margins 1.5-2.5 cm wide, with longitudinal ridges and flaring borders, the valves 2-3 cm wide, flat, concave when young, at maturity convex; seeds 16-24, oblong, surrounded by a thin aril.

Mexico (Oaxaca) to Panama; Trinidad and Tobago. (South America.)

Vernacular names: *tama-tama* (British Honduras—Gentle); *cushin* (Guatemala—Steyermark); *shalum* (Guatemala—Standley); *cuajiniquil* (Salvador—Standley); *guabo cuabrado* (Costa Rica).

MEXICO: CHIAPAS: Finca Yolanda, *C. A. Purpus 6811* (F, GH, MO). OAXACA: Ubero, *Ll. Williams 9136* (F). TABASCO: Teapa, *Linden 726* (K).

BRITISH HONDURAS: Camp 6, Vaca Road, *Lundell 6544* (GH, NY); El Dorado, *Schipp 387* (F); Gracie Rock, Sibun River, *Gentle 1729* (MO, NY); Middlesex, *Hope 1* (F), *Schipp 294* (F, GH, MO, NY, US); Stann Creek, *Burns 11* (F, US); without locality, *Peck 511* (GH).

GUATEMALA: ALTA VERAPAZ: Chamá, *Johnson 892* (US); Gubilgüitz, *Tuerckheim 7855* (US); Sepacuité *Cook & Griggs 13* (US), *631* (US), *706* (US); Yalpemech, *Steyermark 45212* (F). CHIMALTENANGO: Sibajá, *Standley 62555* (F). ESCUINTLA: Pacayal, Santa Emilia, *Bequaert 13* (F, GH). GUATEMALA: Amatitlán, *Popenoe 707* (US); Guarda Viejo, *Kellermann 4397* (US); San Raimundo, *Standley 63036* (F). IZABAL: Los Andes to Entre Ríos,

Record 47 (US); Motagua Valley, *Record & Kuylen 70* (NY, US); Quiriguá, *Standley 24013* (GH, NY, US); Sto. Tomas, Escobas, *Steyermark 39218* (F). JALAPA: El Rancho, *Kellerman 7670* (F, NY). QUEZALTENANGO: Colomba to Asintal, *Standley 87889* (F); Santa María de Jesús to Calahuaché, *Steyermark 33851* (F). RETALHULEU: Retalhuleu, *Standley 88697* (F); Río Samalá, *Shannon 557* (US); San Felipe, *Holway 719* (US). SACATEPEQUEZ: Barranco Hondo, *Standley 60269* (F). SANTA ROSA: Las Viñas, *Heyde & Lux 6095* (F, GH, US). WITHOUT LOCALITY: *Lewton 378* (US).

SALVADOR: LA LIBERTAD: Sta. Tecla, *Levy 785* (EAP), *Williams & Molina s. n.* (F). SAN SALVADOR: San Salvador, *Calderón 117* (GH, US), *171* (GH, NY, US), *1454* (GH, US), *1828* (NY), *Preuss 1386* (photo) (GH, MO), *Renson 239* (US), *Standley 19109* (GH, MO, US), *19198* (GH, US), *20560* (GH, US), *23088* (GH, NY, US), *23641* (GH, NY, US). SAN VICENTE: Apastepeque, *Standley 21342* (GH, US). SONSONATE: Armenia, *Standley 23462* (GH, US); Izalco, *Pittier 1974* (US), *Standley 21803* (GH, US). WITHOUT LOCALITY: *Calderón 2591* (F); *Carlson s. n.* (F).

HONDURAS: ATLANTIDA: La Ceiba, *Yuncker, Koepper & Wagner 8569* (F, GH, NY, US); Tela, *Standley 56845* (F, NY, US). MORAZAN: Montaña Zanquín, *Molina 2980* (F).

NICARAGUA: CARAZO: Diriamba, *Greenman & Greenman 5825* (MO); Jinotepe, *Standley 8449* (F). GRANADA: Volcán Mombacho, *Baker 135* (GH, MO, NY). ZELAYA: Braggman's Bluff, San Antonio, *Englesing 159* (F).

COSTA RICA: ALAJUELA: Nuestro Amo, *Inst. Phys-geogr. C. R. 16915* (K, US); San Ramón, *Brenes 13507* (CR, F, IAIAS); Villa Quesada, *A. Smith 1612* (EAP, F), *1891* (EAP, F, NY). CARTAGO: Juan Viñas, *Cook & Dolye 389* (US); La Gloria, *Pittier 16364* (US); Las Vueltas, Tucurrique, *Tonduz 13055* (GH, NY, US); Río Colorado, Turrialba, *Tonduz 8333* (CR); Turrialba, *León 3922* (IAIAS), *Pittier 9041* (CR, US), *Tonduz 8391* (CR, US). GUANACASTE: Tilarán, La Tejona, *Standley & Valerio 45784* (NY, US). HEREDIA: Heredia, *León 1497* (IAIAS); La Bermúdez. *León 3900* (IAIAS); San Francisco, *León 3812* (IAIAS); San Pablo, *León 3934* (IAIAS); Santo Domingo, *Escheverría 317* (F) *318* (F). LIMON: Cairo, Monte Cristo, *Standley & Valerio 48539* (US). PUNTARENAS: Palmar Norte, *Allen 5785* (EAP, F); Río Ceibo, *Tonduz 4977* (CR); Sto Domingo, Golfo Dulce, *Tonduz 10030* (CR, F, GH, NY, US). SAN JOSE: San Francisco, Guadalupe, *Tonduz 17957* (F, GH, NY, US). WITHOUT LOCALITY: *Inst. Phys-geogr. C. R. 16916* (US).

PANAMA: BOCAS DEL TORO: Almirante region, *Cooper & Slater 65* (US); Changuinola, *Cooper & Slater 108* (F, NY, US), *Dunlap 523* (F, US); Water Valley, *von Wedel 672* (GH, MO), *849* (GH, MO, US), *1822* (MO), *2749* (GH, MO, US). CANAL ZONE: Barro Colorado Island, *Avilés 22* (F), *Bailey & Bailey 410* (F), *Chickering s. n.* (F), *Kenoyer 368* (US), *Killip 40017* (MO, US), *Shattuck 273* (F), *743* (F), *Standley 40992* (US), *Wetmore & Abbe 34* (F, GH), *C. L. Wilson 71* (F), *Woodworth & Vestal 329* (F), *374* (F), *737* (F), *Zetek 3458* (F), *3668* (F), *4398* (F, MO); Daríen Station, *Standley 31610* (US); Empire to Mandinga, *Piper 5112* (US); Las Cruces, *Seemann 407* (GH); Quebrada La Palma, *Dodge & Allen 17340* (F, GH, MO, US); Summit, *Harvey 5180* (F). CHIRIQUI: San Félix, *Pittier 5452* (US). COCLE: Bismarck, above Penonomé, *R. S. Williams 489* (NY). DARIEN: Cituro, *R. S. Williams 673* (NY).

TRINIDAD: without locality, *Ex. Herb. Trin. Bot. Gard. 845* (F), *Hart 895* (F).

TOBAGO: Craig Hall, *Broadway 4355* (F).

The long synonymy of *I. sapindoides* is more the result of detailed work on unstable characters than the existence of determinable variants. In fact no clear-cut entities could be delimited in the available material, and it seems that perhaps the best rank for some of them is a varietal status, as assigned to certain variants by Schery (Ann Missouri Bot. Gard. **37:** 188-225, 1950).

In the whole range of variation some trends may be detected although they lack a firm geographic correlation; the plants of Mexico, Guatemala and Salvador are in general more hairy, while those in Panama, northern South America and Trinidad are often quite glabrous; the length of the calyx and shape of the leaflets are highly variable in the same specimen. A considerable work on the fruit characters shows that certain areas in Costa Rica offer as much variability as

the whole range. The cultivated plants, on the other hand, show a remarkable uniformity, but they may come from a reduced number of progenies.

The most outstanding variant in the area occurs in the Atlantic side of Nicaragua, Costa Rica and Panama, and has been called *I. biolleyana* and *I. panamensis* var. *clavata;* its main characters are the narrowly winged to terete foliar rhachises, the obovate leaflets and elongate corollas. Transitional stages towards other types are frequent and at present it seems scarcely more than a variety.

It is noteworthy to observe that the different synonyms of this species, enumerated above, fall under three different series in the revisions of Pittier. This is partially due to a lack of correlation between the fruit and floral characters, and perhaps also to the poor preservation of some specimens. In résumé it seems more appropriate, until field studies could clarify the validity of the entities, to consider *I. sapindoides* a highly variable species than to accord specific status for the numerous segregates, in which case scores of new species should yet be described based on comparable variants.

Inga sapindoides is often planted as a shade tree in the coffee-growing areas; it has a broad spreading crown, large and well dispersed leaves, and its size is quite favorable to pruning. Its fruits are of rather low quality.

Series 13: INGA

Ser. *Sulcatae* Pittier, Contr. U. S. Nat. Herb. **18**: 210, 1916.

Trees; branchlets terete or angulate, pilose to glabrate. *Leaves* large, pilose, the rhachis terete or winged, the glands crateriform. *Flowers* small to medium size; calyx tubular, pubescent; corolla tubular, appressed-pilose. *Fruit* subterete, the marginal sides broader than the valves, deeply sulcate, often giving a twisted, rope-like appearance to the legume.

This group includes mostly the species of the § INGA of Bentham and constitutes the part of the genus where the variability has reached its highest complexity. The definition of the species becomes very difficult owing to the overlapping of the characters.

It includes in the first place a group of species centering around *I. vera, I. edulis* and *I. oerstediana.* This group is more developed in Mexico and Colombia than elsewhere. In the former country some morphological variants have been described as species, which in the present treatment are reduced mostly under *I. vera.*

A second group is formed by three species without any clear relationship with the first. They are *I. pauciflora, I. brenesii and I. coclensis.* The scanty material available for this latter group does not permit any clear idea of its variability.

SPECIES . . . 40-47

a. Rhachis winged (terete in some specimens of *I. oerstediana*).
  b. Branchlets, leaves and inflorescences densely ferrugineous-hirsute.
    c. Corolla 12-16 mm long; flowers not congested. Panama ......40. I. PAUCIFLORA
    cc. Corolla 20-23 mm long; flowers on short rhachises. Costa Rica 41. I. BRENESII

bb. Branchlets, leaves and inflorescences cinereous-tomentose to glabrescent (often ferrugineous-tomentose in *I. oerstediana*).
  d. Inflorescences spiciform; flowers sessile to very shortly pedicellate.
    e. Calyx 3-6 mm long; legume 8-24 cm long; leaflets oblong to obovate, in 3-4 pairs. Mexico to Panama ....42. I. OERSTEDIANA
    ee. Calyx 8-19 mm long.
      f. Legume 40-120 cm long; leaflets oblong to lanceolate, in 4-6 pairs; bracts lanceolate, 4-6 mm long. Honduras. Costa Rica to Panama ....43. I. EDULIS
      ff. Legume 10-32 cm long.
        g. Bracts ovate-oblong, 9-14 mm long; leaflets obovate to lanceolate, generally in 3-4 pairs. Mexico. ....44. I. LATIBRACTEATA
        gg. Bracts lanceolate, 3-9 mm long; leaflets elliptic to lanceolate, generally in 4-7 pairs. Greater Antilles; Mexico to Panama ....45. I. VERA
  dd. Inflorescences corymbiform; flowers always with well developed pedicels. Guadeloupe to Trinidad ....46. I. INGOIDES
aa. Rhachis terete. Panama ....47. I. COCLENSIS

40. INGA PAUCIFLORA Walp. & Duchass., Linnaea **23:** 746, 1850. (Type *Duchassaing s.n.*)

Small *trees;* branchlets terete, striate, densely ferrugineous-pubescent, in age glabrate, the internodes short. *Leaves* with 3-4 pairs of leaflets; leaflets lanceolate to ovate, acute or acuminate, the base acute to obtuse, asymmetric, above appressed-yellow-pilose when young, in age glabrate and lustrous, the nerves deeply impressed, beneath densely yellow-pilose, the nerves prominent, the upper pair lanceolate-elliptic to broadly elliptic, 9-13 cm long, 4-7 cm wide, the basal pair markedly ovate, 2-5 cm long, 1-2 cm wide, the petiolules less than 1 mm long, conic densely ferrugineous-pubescent; rhachis winged, 3-9 cm long, ferrugineous-pubescent, the glands shortly stipitate, glabrous, retuse; petiole terete, 0.5-1.5 cm long, pubescent; stipules ovate, 4 mm long, ferrugineous-pubescent to glabrous, deciduous. *Inflorescences* solitary or geminate, axillary or terminal; peduncle slender, 1.5-2.5 cm long, densely ferrugineous-pubescent; rhachis hairy, 1-3 cm long, the bracts, obovate, up to 2 mm long, subpersistent. *Flowers* sessile; calyx tubular-funnelform, 8-11 mm long, striate, densely yellow-pubescent, the teeth acute, about 2 mm long, corolla tubular, 12-16 mm long, slightly spreading, appressed-pilose; staminal tube included. *Legume* (immature) terete, curved, up to 14 cm long, 1 cm wide, densely ferrugineous-pilose, ending in a sharp point.

Lowlands of central Panama, apparently common in forests and clearings.

PANAMA: CANAL ZONE: Ancon Hill, *R. S. Williams 32* (NY, US); Barro Colorado Island, *Bangham 462* (F), *Shattuck 1067* (F), *Starry 153* (F), *Woodson & Schery 969* (MO, US), *Zetek 3740* (F), *3907* (F, MO); Chiva-Chiva trail, *Piper 5725* (US). PANAMA: Chorrera to Capira, *Zetek 3927* (F, MO); Panama, *Duchassaing s. n.* (GH). VERAGUAS: Santa Fé, *Allen 4417* (MO).

Bentham (Trans. Linn. Soc. **30:** 627, 1875) reduced *I. pauciflora* to synonymy with *I. vera*, basing this assumption on the Duchassaing collection alone. Pittier (Contr. U.S. Nat. Herb. **18:** 214, 1916) reinstated its specific value, and put it

among his EUINGA-SULCATAE. In this series it does not have any close allies, but the fruit and flower characters do not leave any doubt about its place in the series INGA (i.e. SULCATAE Pittier).

41. INGA BRENESII Standley, Publ. Field Mus. Nat. Hist., Bot. Ser., **18:** 495, 1937. (Type *Brenes 5121*)

Trees 5 to 8 m tall; branchlets angulate, densely ferrugineous-tomentose, lenticellate. *Leaves* with 3 pairs of leaflets; leaflets obovate to elliptic, coriaceous, the margins revolute, the apex acute to mucronate, cuneate at the base, above lustrous, glabrous, but sparsely pilose along the impressed nerves and on the margin, beneath dull, dark, pilose, the nerves very prominent, the upper pair obovate 9-13 cm long, 4-8 cm wide, median and lower pairs elliptical, sometimes asymmetric, the basal pair 5-7 cm long, 2-3 cm wide, the glands small, shortly stipitate, glabrous; petiole angulate, sometimes winged, 1.5-2.5 cm long, densely ferrugineous-pubescent; stipules ovate, short, 3-4 mm long, persistent. *Inflorescences* axillary; peduncle terete, 2-4 cm long, striate, densely ferrugineous-pilose; rhachis 1.0-1.5 cm long, the bracts rhombic, acute, about 4 mm long, pubescent. *Flowers* sessile, congested, giving an umbellate appearance to the inflorescences; calyx tubular, 9-12 mm long, densely ferrugineous-pubescent, the teeth short and obtuse; corolla tubular-funnelform, 20-23 mm long, densely pilose, the lobes 3-6 mm long; staminal tube included; ovary thick, glabrous. *Legume* unknown.

Wet forests of the central highlands of Costa Rica.

Vernacular name: *guabo peludo* (Costa Rica–Brenes).

COSTA RICA: ALAJUELA: La Palma, San Ramón *Brenes 5121* (CR, F), *4988* (CR, F, IAIAS).

Inga brenesii is placed in the series INGA on the basis of its similarity to *I. pauciflora* in foliar and floral characters, since its fruit is unknown. The thick ovary also suggests that the legume may be subterete, and according to the other characters it is difficult to place in any other series.

42. INGA OERSTEDIANA Benth. ex Seem., Bot. Voy. Herald 117, 1853. (Type *Oersted 12*)

Feuilleea oerstediana (Benth.) O. Ktze., Rev. Gen. Pl. **1:** 188, 1891.
Inga eriorhachis Harms in Fedde, Rep. Sp. Nov. **13:** 525, 1915. (Type *Tonduz 1214*)
I. cobanensis Pittier, Contr. U. S. Nat. Herb. **18:** 188, 1916. (Type *Tuerckheim 11630*)
I. tuerckheimii Pittier, loc. cit. 192. (Type *Tuerckheim 1214*)
I. edulis Mart. var *grenadensis* Urb. in Fedde, Rep. Sp. Nov. **15:** 307, 1918 (ex char.; Type *Eggers 6384, not seen*)
I. culagana Britton & Killip, Ann. N. Y. Acad. Sci. **35:** 115, 1936. (Type *Killip & Smith 20165*)
I. pamplonae Britton & Killip, loc. cit. 119. (Type *Killip & Smith 19777*)
I. chartana Britton & Killip, loc. cit. (Type *Killip & Smith 19088*)
I. chiriquensis Standley, Publ. Field Mus. Nat. Hist., Bot. Ser., **22:** 78, 1940. (Type *Davidson 928*)
I. edulis Mart. var. *minutiflora* Schery, Ann. Missouri Bot. Gard. **37:** 109, 1950. (Type *Allen 968*)

Trees 6 to 18 m tall; branchlets terete or angulate, densely ferrugineous- or cinereous-tomentose. *Leaves* with 3-4 (rarely 5) pairs of leaflets; leaflets subchartaceous, oblong to obovate, the apex obtuse to shortly acuminate, the base rounded or cuneate, often oblique, above dull, sparsely pilose, the nerves slightly prominent and tomentose, beneath densely ferrugineous- or cinereous-tomentose, the lateral nerves straight, anastomosing close to the margin and with the tertiary nervation transverse and conspicuous, the upper pair elliptic to obovate, 8-22 cm long, 4-12 cm wide, the intermediate pair slightly smaller, often oblique, the basal pair ovate to lanceolate, 4-13 cm long, 3-8 cm wide (the dimension and shape of the leaflets are quite variable in the same branchlet), the petiolules conic, 1-2 mm long, densely tomentose; rhachis terete, subalate, or markedly winged, 7-22 cm long, densely tomentose on the midrib, the wings elliptic, each up to 1.5 cm wide (saccate at the base in some Guatemalan specimens), the glands large, patelliform to crateriform, circular or triangular, at the border with the rim fleshy and narrower at the sides; petiole terete or winged, 2-7 cm long, densely tomentose; stipules ovate, 2-3 mm long, pubescent, caducous. *Inflorescences* 1-4, axillary, fasciculate or paniculate on short axes; peduncle terete, stout, 1-4 cm long, densely ferrugineous- or cinerous-tomentose; rhachis 1-4 cm long, the bracts reniform to ovate, 1-4 mm long, caducous. *Flowers* sessile, not congested; calyx cupulate-tubular, 3-6 mm long, densely tomentose, the teeth 1-2 mm long, often irregular; corolla tubular, spreading above, 9-15 mm long, appressed-pilose, the lobes acute, 2-3 mm long; staminal tube included to exserted, the filaments about 1.0-2.5 cm long; ovary oblong, glabrous. *Legume* terete, oblong, 8-24 cm long, 1.0-2.5 cm in diam, densely ferrugineous- or cinereous-tomentose, at maturity the margins rather straight.

Mexico to Panama; West Indies, from sea level to 1800 m elevation. (South America.)

Vernacular names: *jaquinicuil* (Mexico-Hinton); *cushin* (Guatemala-Standley); *guama pachona* (Honduras - von Hagen); *cuajiniquil peludo* (Costa Rica).

MEXICO: GUERRERO: Minas, Pilas, *Hinton 10746* (F, GH, K, MO, NY, US). OAXACA: Cafetal Concordia, *Ll. Williams 9380* (F, MO); Ubero, *Morton & Makrinius 2496* (F, US).

BRITISH HONDURAS: Middlessex, *Schipp 383,* (F, GH, MO, NY, US); Stann Creek, *Gentle 3020* (K, NY).

GUATEMALA: ALTA VERAPAZ: Carchá, Chicoj, *Standley 70045* (F); Cobán, *Standley 69543* (F); Cobán to San Pedro Carchá *Standley 90017* (F); Samac, NW of Cobán, *Standley 89677* (F), *89708* (F, US); San José, SE of Tactic, *Standley 69621* (F); Sepacuité, *O. F. Cook 124* (US), *Cook & Griggs 50* (US), *227* (US), *228* (US), *620* (US); Tactic, *Popenoe 781* (US), *Standley 92509* (F); Tactic to Tamahu, *Standley 71260* (F), *91364* (F). CHIMALTENANGO: Chimaltenango to San Martín, Jilotepeque, *Standley 64478* (F). ESCUINTLA: Barranco Hondo, above Las Lajas, *Standley 63873* (F). QUEZALTENANGO: Colomba, road to Asintal, *Standley 87910* (F); San Lorenzo, El Cubo, *L. O. Williams 13208* (F); Volc. Sta. María, Sta. María de Jesús to Calahuaché, *Steyermark 33716* (F). SACATEPEQUEZ: Cerro de La Cruz, Antigua, *Standley 63336* (F); Dueñas, *Standley 63131* (F, NY). SUCHITEPEQUEZ: Mocá, *Bequaert 56* (F, GH). PROVINCE UNKNOWN: San Miguelito, Santa Rosa, *Bernouilli & Cario 1252* (K); Esperanza, *Maxon & Hay 3355* (US).

SALVADOR: AHUACHAPAN: Ataco, *Standley & Padilla 2733* (F). LA LIBERTAD: Finca Germania, near Comasagua, *Carlson 206* (F); Santa Tecla, *Levy 786* (EAP). SAN SALVADOR: Volc. San Salvador, *Calderón 1564* (GH, US). SANTA ANA: Finca Pilón, Los Naranjos, *Williams, Molina & Levy 15168* (F, EAP).

Honduras: atlantida: Lancetilla, *Yuncker 4922* (F, MO); Tela, *Standley 53601* (F, GH, MO, NY, US), *56548* (F), *56617* (F). colon: Tanjica, near Trujillo, *Bangham 250* (F). el paraiso: Güinope, *Standley & Williams 4556* (F). *Williams & Molina 11993* (F, GH). morazan: La Montañita, *Williams & Molina 21669* (F, GH); La Montañita, above Suyapa, *Williams 15745* (EAP, F, US). yoro: Pijol, Subirana, *von Hagen 1117* (F, NY); Subirana, *von Hagen & von Hagen 1071* (F, NY).

Nicaragua: managua: Casa Colorada, *Maxon, Harvey & Valentine 7384* (US); Crucero, *Standley 8221* (F); Managua, *Garnier 1062* (US). zelaya: El Recreo, *Standley 19126* (F), *Lewis 38* (F).

Costa Rica: alajuela: La Tigra, San Carlos, *Barquero 12* (IAIAS, MO); San Pedro, San Ramón *Brenes 5495* (CR, F, IAIAS); Zarcero, *A. Smith 121* (F, MO). cartago: Aguacaliente, *Pittier 2372* (CR, US), *Torres 82* (F); Cartago, *Cook & Doyle 19* (US) *20* (US); Dulce Nombre, *Standley 35820* (US); Las Cóncavas, *Pittier 16661* (GH, US); Las Vueltas de Tucurrique, *Tonduz 12745* (CR, NY, US); Tres Ríos, *León 1235* (CR); Turrialba, *Holdridge 2549* (IAIAS), *León 1533* (IAIAS). heredia: Barba, *León 3926* (IAIAS); Heredia, *León 1498* (IAIAS); Río Ciruelas, *Tonduz 2236* (CR, US); San Francisco, *León 3807* (IAIAS); Santo Domingo, *Echeverria 316* (F). limon: Guácimo, *United Fruit Co. 144* (US); Suerre, *J. D. Smith 6491* (US). san jose: Belmira de Dota, *Tonduz 11636* (CR, GH, MO, US); Candelaria, *Oersted 12* (K), *4420* (F, K); Copey, *Tonduz 11683* (CR, GH, K, NY, US); San Pedro de Coronado, *M. Valerio 1737* (F); Santa María de Dota, *Standley & Valerio, 44123* (NY, US); Vueltas de Jorco, *León 3828* (IAIAS), *3831* (IAIAS).

Panama: bocas del toro: Changuinola Valley, *Dunlap 582* (F); Cricamola, *G. P. Cooper 527a* (F). canal zone: Barro Colorado Island, *Bangham 395a* (F), *Bailey & Bailey 345* (F), *670* (F), *M. Brown 129* (F), *Chickering 56* (F), *Kenoyer 371* (US), *Shattuck 426* (F), *Standley 31236* (US), *Starry 216, Wetmore & Abbe 72* (F, GH), *Woodworth & Vestal 361* (F), *Zetek 3578* (F), *3619* (F); Gamboa, *Allen 1972* (GH, MO, NY, US); Gorgona, *Pittier 2696* (F, GH, NY). chiriqui: Boquete, *Davidson 536* (F, MO) *928* (F, MO), *Pittier 3130* (NY, US); Cerro Punta, *Allen 1573* (GH, NY, US). darien: El Real, *Allen 968* (GH, MO, US).

Grenada: Ammandale, *Broadway s. n.* (F, NY); Balthazar, *J. S. Beard 197* (MO); without locality, *Eggers 6236* (US).

Tobago: The Widow, Three Flowers, *Broadway 4659* (MO, NY, US).

The specific delimitation of *I. oerstediana* here offered includes some entities attributed up to now to *I. edulis,* which were separated from the former on the color of the indument alone. It seems now that they are forms occurring at different elevations and that plants from the cloud forest possess in general a thicker and ferrugineous indument while in those growing at lower elevations the hairs are cinereous and more sparsely distributed.

The species itself is quite variable and some of the entities among those reduced to synonymy are local variants: 1) Some populations of Guatemala, Salvador and Honduras that fall under *I. cobanensis* (commonly classified as *I. micheliana*) have somewhat smaller calyces and leaves than the typical plants, but intergrade well within the specific variability. 2) Plants from the highlands of Mexico, Guatemala, Costa Rica and Panama are very similar, corresponding to the typical population. *Inga eriorhachis,* in which the rhachis is completely terete, is a form occurring in Costa Rica, but it seems that rhachial parts are particularly variable in *I. oerstediana.* 3) Included in this species are two varieties, one from Grenada and Tobago (*I. edulis* var. *grenadensis* Urb.) and another from Panama (*I. edulis* var. *minutiflora* Schery). These seem to have no apparent relation to the typical populations of *I. edulis* that occur in South and Central America, but are close to the *I. oerstediana* complex, especially to those variants occurring in the lowlands.

In South America *I. oerstediana* is known definitely from Venezuela to Ecuador

but probably *I. endlicheri* (O. Ktze.) Macbride, described by Poeppig as *I. fasciculata,* and some specimens from northern Bolivia may belong to the same species.

As noted above, the separation of *I. oerstediana* and *I. edulis* in herbaria is rather confused. The study of many specimens and mass collections seems to clarify the two concepts as far as *I. edulis* var. *typica* is concerned. The striking differences are in calyx size, shape and number of leaflets, size of bracts and probably the length of the legumes, and do not offer any important overlapping between the typical populations of *I. edulis* and *I. oerstediana.*

Inga oerstediana is often planted in Central America as a shade tree in the coffee and cacao groves. The fruits, although edible, are of rather poor quality. Standley and Steyermark report the use of the leaves in Guatemala, to wrap "tamales" to which they impart a purplish tinge much admired by the local people.

43. Inga edulis Mart., Flora **20:** Beibl. 113, 1837. (Based on *Mimosa ynga* Vell.).

Mimosa ynga Vell., Fl. Flum. Ic. 11, *t.* 3, 1827. (ex ic.)
Inga vera H.B.K., Nov. Gen. Sp. Pl. **6:** 289, 1827, non Willd. (*fide* Bentham).
I. ynga (Vell.) J. W. Moore, Bernice P. Bishop Mus. Occ. Pap. 10, **19:** 6, 1934.

Trees 6 to 15 m tall; branchlets terete or angulate, densely tomentose. *Leaves* with 4-6 (generally 5) pairs of leaflets; leaflets subchartaceous, oblong to lanceolate, the apex acute, narrowly acuminate to mucronate, the base rounded, above minutely and sparsely pubescent to scabrous, the nerves slightly prominent and more pilose, beneath paler, sparsely pilose, the nerves prominent, the upper pair narrowly elliptic to rhombic, 8-18 cm long, 3-8 cm wide, the basal pair lanceolate, 3-7 cm long, 2-4 cm wide, the petiolule conic, 1-2 mm long, densely pilose; rhachis winged, 6-14 cm long, the wings cuneate, the glands patelliform to crateriform, the rim fleshy, thinner at the sides; petiole terete, 2-6 cm long, densely tomentose, the pulvinar section thicker; stipules broadly ovate, about 3 mm long, pilose, caducous. *Inflorescences* 1-6, axillary, paniculate; peduncle terete or angulate, rather slender, 2-6 cm long, striate, tomentose; rhachis 3-4 cm long, the bracts lanceolate, 4-6 mm long, caducous. *Flowers* sessile, distant on the lower part of the rhachis, congested above; calyx tubular, 7-9 mm long, cinereous-tomentose, the teeth obtuse, 1-2 mm long; corolla tubular, 14-20 mm long, appressed-pilose, the lobes acute, 2-5 mm long, spreading; staminal tube included to exserted, the filaments 2-3 cm long; ovary oblong, glabrous, the style about 3.5 cm long. *Legume* markedly sulcate, up to 120 cm long.

Honduras (cultivated?) to Panama. (South America.)

Vernacular name: *guabo mecate* (Costa Rica and Panama).

Honduras: Morazan: El Zamorano, *Standley 13079* (F), *16086* (EAP, F).

Costa Rica: alajuela: La Paz, San Ramón, *Córdoba 187* (IAIAS), *189* (IAIAS). cartago: Instituto de Ciencias Agrícolas, Turrialba, *Córdoba 92* (IAIAS); La Dominica, Turrialba, *León 3952* (IAIAS). heredia: La Bermúdez, *León 3832* (IAIAS); San Francisco, *León 3817* (IAIAS), *3818* (IAIAS). limon: Shirores, *Tonduz 9357* (CR, US). puntarenas: Boruca, *Tonduz 4710* (CR); Térraba, *León 1136* (CR), *Tonduz 3825* (CR).

Panama: bocas del toro: Almirante, *Cooper & Slater 38* (US); Changuinola Valley, *Dunlap 220* (F, MO); Chiriqui Lagoon, *von Wedel 1000* (GH, MO); Water Valley, *von Wedel 1096* (GH, MO).

Inga edulis is a South American species well known in Brazil as a fruit tree. It is doubtful whether this species is native in Central America, for apparently all collections come from trees close to old or new settlements. This *Inga* produces large fruit up to a meter long; nowhere in Central America, however, do they reach the size and quality as in South America. It is also commonly planted as shade trees in coffee and cacao fields, since it has a well spreading crown and produces large quantities of leaves which cover the ground and add considerable quantities of organic matter to the soil.

Inga edulis is exceedingly variable. In the same field where they are cultivated for shade, it is possible to detect individuals with small or large leaflets, with long or relatively short fruits, with dense or open foliage. It is also quite possible that hybridization among these individuals as well as with other species, like *I. oerstediana,* may be the factor that determines its high variability.

44. Inga latibracteata Harms in Fedde, Rep. Sp. Nov. **19:** 64, 1923. (Type *Pringle 8159*)

I. sciadodendron Harms in Fedde, loc. cit. 62. (Type *J. A. Purpus 279* photo)
I. zapacuanica Harms in Fedde, loc. cit. 63. (Type *C. A. Purpus 3684*)
I. endlichii Harms in Fedde, loc. cit. (ex char.; Type *Endlich 1536,* not seen)

Trees; branchlets terete, when young densely ferrugineous-tomentose, in age glabrescent and lenticellate. *Leaves* with 3-5 (generally 4) pairs of leaflets; leaflets elliptic to lanceolate, the apex acute to obtuse, generally shortly mucronate, the base obtuse to rounded or somewhat cordate, above scabrous-pilose, opaque, the nerves and costa slightly prominent and more pubescent, beneath ferrugineous-tomentose, the lateral nerves markedly prominent, the upper pair cuneate-elliptic to obovate, 12-17 cm long, 5-9 cm wide, the lower pair lanceolate to elliptic, 5-7 cm long, 3-4 cm wide, the petiolules conic, 2-3 mm long, ferrugineous-tomentose; rhachis winged, 6-12 cm long, the wings elliptic and pubescent, the glands patelliform, sessile, 1-2 mm in diam; petiole often terete, rarely winged, 2-5 cm long, densely ferrugineous-tomentose. *Inflorescences* 1-3 per axil, rarely terminal; peduncle terete, tomentose, 3-5 cm long; rhachis 2-4 cm long, the bracts lanceolate to ovate, 7-12 mm long, pubescent, caducous. *Flowers* rather loose, sessile; calyx tubular, 7-12 mm long, tomentose, the teeth acute, 2-4 mm long; corolla tubular, spreading above, 12-20 mm long, appressed-pilose, the lobes acute, 3-4 mm long; staminal tube included to exserted. *Legume* (immature) subterete, 10-22 cm long, sulcate, densely ferrugineous-tomentose.

Highlands of Veracruz.

Mexico: veracruz: Jalapa, *Pringle 8159* (F, GH, MO), *C. L. Smith 1690* (EAP, NY), *Schiede s. n.* (GH); Mirador, *J. A. Purpus 279* (photo NY); Misantla, *Schiede s. n.* (GH); Orizaba, *Botteri 365* (GH); Zacualpán, *C. A. Purpus 3684* (F, MO), *8765* (GH, MO, NY), *10698* (F, NY), *10700* (NY), *10964* (F), *14036* (F, NY).

Inga latibracteata is a highly variable species confined in geographic distribution to the highlands of Veracruz. The populations are so variable that the few specimens available are different from one another but intergrade in important

characters among themselves, and for this reason have been reduced into one species.

The limits of *I. latibracteata* are not clear. On one hand it merges into the vast complex of *I. vera* subsp. *spuria*, as in the case of the type of *I. zapacuanica*, while on the other hand it is closely related to the Central American *I. oerstediana* in the size and shape of the leaflets, flowers and pods, as well as in the ferrugineous tomentum found upon all parts of the plants. The striking variability may suggest a hybrid origin or that we are dealing here with immature species in process of evolution. It would be highly desirable to obtain population samples in order to ascertain the nature of this interesting problem.

45. Inga vera Willd. in L., Sp. Pl. **4:** 1010, 1806. (Based on *Mimosa inga* L.)

Mimosa inga L., Sp. Pl. 1498, 1753, non Vell. (Based on Sloane, Hist. **2:** 58, *pl. 183, fig. 1, 1629*)

Trees; branchlets terete, pubescent to glabrate, lenticellate. *Leaves* obovate to lanceolate, the apex rounded to acuminate, rarely mucronate, the base acute to rounded, above sparsely pilose, opaque, the nerves slightly prominent, beneath more densely pilose or tomentose, the nerves prominent, the upper pair obovate to narrowly elliptic, 3-22 cm long, 2-9 cm wide, the basal pair lanceolate, 2-12 cm long, 1-6 cm wide, the petiolules short, conic, 1-4 mm long, densely pilose; rhachis winged, 4-14 cm long, pubescent on the midrib, the wings elliptic or cuneate, the glands patelliform, circular or triangular in outline, less than 2 mm wide; petiole terete or winged, 2-4 cm long, pilose to glabrescent; stipules ovate to lanceolate, 3-7 mm long, caducous. *Inflorescences* axillary or terminal, 1 to many, fasciculate or paniculate; peduncle terete, 4-8 cm long, pubescent; rhachis 2-6 cm long, the lower flowers distant, congested above, the bracts reniform to lanceolate, 3-11 mm long, caducous or subpersistent. *Flowers* sessile to shortly pedicellate, few to many, distant or congested; calyx cylindric to turbinate, 9-18 mm long, 5-7 mm wide, pilose to tomentose, the pubescence ferrugineous to cinereous; corolla tubular, spreading above, 9-22 mm long, appressed-pilose; staminal tube included to exserted. *Legume* subterete, sulcate, straight or curved, 12-22 cm long, densely tomentose to glabrescent.

Mexico to Panama; Jamaica to Puerto Rico. (South America.)

Inga vera, the type species of the genus, is also the most complex within it. Its origin is probably South American. In the Greater Antilles minor variations are observed from one island to the other, but its main variants in this area also are found on the Continent. Within the whole range, from Mexico to Panama, it is possible to observe numerous variants, some of which have received specific rank. After long study the conclusion reached agrees with the old opinion of Bentham that despite the high variability, the different morphological types can be grouped under a rather small number of subspecific populations. Three of them are recognized here: one in the Greater Antilles, a second in western Mexico, and a third from eastern Mexico to Panama. (South America.)

The reduction under one species of the many types found, especially in

Middle America, has been done in the past by Harms, Taubert, J. D. Smith, etc., contrary to the view of Pittier who not only considered the Central American plants distinct from those of the Caribbean, but divided the former into several species. If these small units are accepted it will be necessary to multiply the number of species *ad infinitum*, and to recognize as such the many other variants that occur in the area.

Key to the Subspecies

a. Calyx cylindric, 10-14 mm long, 4-6 mm wide; leaflets of the upper pair broadly elliptic to obovate, sparsely pilose to almost glabrous. Jamaica, eastern Cuba, Hispaniola, and Puerto Rico .... 45a. I. vera subsp. vera

aa. Calyx turbinate or subcylindric; leaflets of the upper pair narrowly elliptic or obovate to falciform, sparsely to densely pilose.

- b. Calyx short and broad, the width at the mouth one half or more the length; floral peduncles less than 4 cm long, stout; bracts oval to reniform, less than 6 mm long; leaflets generally in 4 (2-5) pairs; pubescence of the branchlets, leaves and flowers, ferrugineous. Highlands of Mexico, from Sinaloa to Morelos and Chiapas .... 45b. I. vera subsp. eriocarpa
- bb. Calyx elongate; floral peduncles slender and long, 5-7 cm long; bracts lanceolate, 6-9 mm long; leaflets generally in 6 (5-9) pairs; pubescence of the branchlets, leaves and flowers commonly cinereous (or ferrugineous in plants found at high altitudes). Mexico: Coahuila and Tamaulipas to Tabasco on the eastern side, lowlands of Guerrero to Chiapas in the western side; Guatemala to Panama .... 45c. I. vera subsp. spuria

45a. Inga vera Willd. subsp. vera.

I. lamprophylla C. Wright in Benth., Trans. Linn. Soc. **30:** 627, 1875, nom. nud. pro syn. (Type *Wright, Parry & Brummel 68*)
Feuilleea inga (L.) O. Ktze., Rev. Gen Pl. **1:** 184, 1891.
Inga vera Willd. subsp. *lamprophylla* (C. Wright) Pittier, Contr. U. S. Nat. Herb. **18:** 216, 1916.
I. vera Willd. subsp. *portoricensis* Pittier, loc. cit. 217. (Type *Heller 4471*)
I. inga (L.) Britton, Fl. Bermuda 170, 1918.
I. vera Willd. var. *lamprophylla* (C. Wright) Macbride, Contr. Gray Herb. n.s. **59:** 1, 1919.
I. vera Willd. var. *portoricensis* (Pittier) Macbride, loc. cit.

Trees; branchlets terete, striate, ferrugineous-tomentose to glabrate, lenticellate. *Leaves* with 3-6 (generally 4-5) pairs of leaflets; leaflets broadly elliptic to lanceolate, the apex acute to long-acuminate, the base cuneate to rounded, above sparsely pilose to glabrescent, the nerves slightly impressed and more pilose, beneath sparsely and shortly pubescent to almost glabrous, the nerves prominent, the upper pair broadly elliptic to rhombic, 8-13 cm long, 4-6 cm wide, the basal pair lanceolate, 4-5 cm long, 2-3 cm wide, the petiolules about 1 mm long, densely pilose; rhachis winged, 6-4 cm long, tomentose on the midrib, the wings cuneate, the glands patelliform, sessile to very shortly stipitate, about 1 mm in diam; petiole terete, or winged above, 1-2 cm long, pilose, the pulvinus darker and thicker; stipules lanceolate, acute, 4-6 mm long, caducous. *Inflorescences* axillary or terminal, 1-4; peduncle slender, 2-5 cm long, tomentose to glabrescent; rhachis 2-4 cm long, the bracts lanceolate, 3-4 mm long, caducous. *Flowers* sessile or very shortly pedicellate, distant in the lower part of the rhachis, congested in the upper part; calyx cupulate-tubular, 8-14 mm long, tomentose, the teeth acute,

3-4 mm long; corolla tubular, dilating above, 14-17 mm long, appressed-pilose, the lobes acute to obtuse, 3-4 mm long; staminal tube included to slightly exserted, the filaments about 4 cm long. *Legume* sulcate, 10-15 cm long, 1-2 cm wide.

Jamaica, eastern part of Cuba, Hispaniola, Puerto Rico.

Vernacular name: *guaba* (Puerto Rico–Britton).

JAMAICA: HANNOVER: mouth of Río Grande, *A. E. Wight 141* (F, NY). PORTLAND: Moore Park to Portland, *Harris 6613* (US); Port Antonio, *Fredholm 3204* (US), *Hitchcock s. n.* (MO). ST. ANN: New Ground, *Harris 10364* (F, NY, US); New Grounds River, *Britton 2494* (NY). ST. MARY: Castleton, *Fawcett 8013* (F, NY). ST. THOMAS: Bath, *Britton 3489* (NY); Port Morant, *Hitchcock s. n.* (MO); Spring, St. Thomas, *Harris 5406* (US); WITHOUT LOCALITY: *Alexander s. n.* (NY), *Griseb. Fl. W. Ind. 471* (GH), *Hart 1025* (US), *1026* (US).

CUBA: ORIENTE: Joturito, *Ekman 16046* (US); San Juan Hill, *Shafer 12420* (MO, NY, US); Santiago, *Havard 109* (NY).

HAITI: ARTIBONITE: Ennery, *Ekman 9669* (US); Gros Morne, *E. C. Leonard 9825* (GH, US); Marmelade, *E. C. Leonard 8351* (US), *8355* (US), *Nash 686* (NY); Petit Rivière, *Sweet 7* (US); St. Marc, *E. C. Leonard 2952* (GH, NY, US); St. Michel de l'Atalaye, *E. C. Leonard 7510* (NY, US), *Miller 293* (US). NORD: Bayeux, near Port Margot, *Nash 337* (F, NY). NORD-OUEST: Jean Rabel *Leonard & Leonard 13809* (GH, NY, US), *12677* (US); St. Louis du Nord, *Leonard & Leonard 14215* (US). OUEST: Port-au-Prince, *Jaeger 109* (GH, NY, US). WITHOUT LOCALITY: *Buch 317* (US).

DOMINICAN REPUBLIC: ALTA GRACIA: Higuey, *Taylor 392* (F, NY). AZUA: Azúa, *Rose, Fitchell & Russell 3987* (NY, US). BARAHONA: Barahona, *Fuertes 50* (NY, US); Paraíso, *Abbot 1648* (US); Pedernales to Aceital, *Howard & Howard 8239* (GH) SAN JUAN: El Cercado, *Howard & Howard 8667* (GH); Río Juan, *Miller 1254* (US). LA VEGA: Jarabacoa: *Allard 14841* (US). PUERTO PLATA: La Cumbre, *Raunkiaer 1251* (US). SAMANA: Samaná, *Wright, Parry & Brummell 68* (GH, US); Sánchez, *Abbott 78* (GH, US). SEIBO: Jovero, *Abbot 2544* (US). SANTO DOMINGO: Santa Domingo, *Schiffino 166* (GH); Haina, *Farris 531* (US). WITHOUT LOCALITY: *Scarff s. n.* (F), *Prenleloup 146* (NY, US).

PUERTO RICO: AGUADILLA: Maricao, *without collector,* (NY). ARECIBO: Utuado, *Britton & Cowell 402,* (F, NY). GUAYAMA: Agua Buena to Caguas, *Sintenis 2545* (US); Aibonito, *Heller 867* (F, NY, US); Caguas, *Underwood & Griggs 355* (US); Cayey, *Kuntze 403* (NY). HUMACAO: Río Icaco, S of Naguabó, *Shafer 3178* (NY, US), *3183* (NY); Sierra de Luquillo, *Sintenis 1533* (US). MAYAGUEZ: Las Mesas, *Holm 259* (F, GH, MO, NY); Mayagüez, *Heller 4471* (F, GH, MO, NY), *Otero & Gregory 1018* (US), *Sintenis 47* (GH); San Germán, *Miller 1663* (US); Yauco, *Sargent 520* (US). SAN JUAN: Bayamón, *Stahl 215* (US); Río Piedras, *Otero 227* (MO). PROVINCE UNKNOWN: Monte Llano, *Goll, Cook & Collins 465* (US); Quebrada Averias, *Goll, Cook & Collins 330* (NY); El Duque, *Stevenson 510* (US).

The variability of *I. vera* subsp. *vera* is rather reduced, although the plants present slight variations from island to island. This range, however, does not justify the creation of different entities. The most striking trends seem to be towards tubular calyces and broad leaflets, scarcely pubescent to almost glabrous in some Jamaican specimens. The plants in general are very similar to some collections from Mexico and Honduras; this fact, and their absence in the Lesser Antilles, seem to suggest that the Antillean plants came from the continent via Central America, and have developed their characteristics through a long isolation.

Linnaeus based his *Mimosa inga* partially on material from this area, described by Sloane, of which only a fruit is preserved. The illustration in the Hist. of Jamaica, *pl. 183, fig. 1,* 1629, is rather inaccurate, since it shows a terminal leaflet, but the fruit is in general well represented.

45b. INGA VERA Willd. subsp. **ERIOCARPA** (Benth.) J. León, stat. nov.

I. eriocarpa Benth. in Hook., Lond. Jour. Bot. **4:** 615, 1845. (ex char.; Type *Coulter s.n.*, not seen)
I. oophylla Riley, Kew Bull. **1923:** 401, 1924. (Type *González Ortega 250*)

Trees; branchlets terete or angulate with short internodes, densely ferrugineous-tomentose when young, glabrate and lenticellate in age. *Leaves* with 2-5 (generally 4) pairs of leaflets; leaflets subcoriaceous, obovate to broadly lanceolate, the apex acute to rounded, often curved, the base cuneate to rounded, above dull, gray to green when dry, covered with sparse, short and yellow hairs, the nerves slightly prominent and more pilose, beneath paler, densely to sparsely ferrugineous-tomentose, rarely glabrous, the nerves prominent, the upper pair obovate to elliptic, generally 6-11 cm long, 2-5 cm wide, the basal pair lanceolate, about half the size of the upper pair; rhachis winged, 4-9 cm long, densely tomentose on the midrib, the glands sessile, patelliform, less than 2 mm in diam; petiole terete or winged, 1.5-4.0 cm long, the pulvinus conic and thicker. *Inflorescences* axillary or terminal; peduncle stout, less than 4 cm long, densely ferrugineous-tomentose; rhachis about 3 cm long, the lower flowers rather distant, the upper congested, the bracts ovate to reniform, up to 6 mm long, densely ferrugineous-tomentose, caducous. *Flowers* sessile to markedly pedicellate; calyx turbinate, broad, the width always more than half the length, 8-12 mm long, 6-8 mm wide at the base of the teeth, densely ferrugineous-tomentose; corolla tubular, well exserted, 14-22 mm long, appressed-pilose, the lobes obtuse, 5-6 mm long; staminal tube included, the filaments about 3 cm long. *Legume* sulcate, straight or curved, 12-22 cm long, 1-2 cm in diam, densely ferrugineous-tomentose.

Southern and western slopes of the central highlands of Mexico, from Durango and Sinaloa to Morelos and Chiapas.

MEXICO: CHIAPAS: San Vicente, *Goldman 858* (US). DURANGO: Sierra Tres Picos, *Gentry 5317* (MO). GUERRERO: Acapulco, *Palmer 250* (F, GH, MO, NY, US); Achotla, *Reko 4911* (US); Coyuca, *Hinton 5527* (MO, NY, US); Jaripo, *Hinton 6483* (MO, US); Manchón, Mina, *Hinton 9248* (F, GH, MO, NY, US), *9259* (F, GH, MO, NY, US), *10074* (F, GH, MO, NY); Placeres, Mina, *Hinton 9089* (F, GH, MO, NY, US), *9997* (F, GH, MO, NY, US); San Luís de La Loma, *Langlassé 932* (GH, US); Taxco, *Abbot 100* (GH), *100a* (GH), *Lyonnet 668* (MO, NY, US); Tecpán, El Reparo, Galeana, *Hinton 14125* (US). JALISCO: Guadalajara, *Safford 1414* (US); La Palma, *M. E. Jones 183* (MO, US); San Sebastián, *Mexia 1842* (F, GH, MO, NY, US); Talpa to Mascota, *Nelson 4042* (GH, US). MEXICO: Acatitlán, Temascaltepec, *Hinton 3159* (MO, US), *5572* (F), *6184* (MO, NY, US); Ixtapán, Temascaltepec, *Hinton 6205* (F); Tejupilco, Temascaltepec, *Hinton 3981* (MO, NY), *6232* (F, US), *7349* (MO, US); Temascaltepec, *Hinton 5911* (F), *8977* (MO, NY, US). MICHOACAN: Apatzingán, El Capire, *Leavenworth 445* (F, GH); Coalcomán, *Hinton 12942* (GH, NY, US); Hacienda Coahuayula, *Emrick 22* (F); Los Reyes, *Nelson 6844* (GH, US); Sta. Inés, *Langlassé 34* (GH, US); Torrecillas, Coalcomán, *Hinton 13718* (NY, US). MORELOS: Cuernavaca, *Bilimek 936* (GH, NY, US), *Froderstrom & Hultén 456* (NY), *Leavenworth 930* (F), *Reko 4649* (US), *Rose & Hough 4361* (US); San Antón, Cuernavaca, *Seler 4183* (GH). NAYARIT: Acaponeta, *Lamb 536* (NY, US), *Rose 1437* (GH, NY, US), *Rose, Standley & Russell 14181* (NY); Cortina, *Gonzalez Ortega 14* (US); Esperanza, Mina, *González Ortega 6660* (US); Ixlán, *Viereck 1165* (US); La Labor, *Collins & Kempton 78* (US); Pedro Paulo, *Rose 3328* (US); Río Grande, E of Santiago, *Gregg 1060* (MO); Río San Pedro, vers. W de la Sierra, *Diquet s. n.* (NY); San Leonel, *Gregg 978* (MO); Tepic, *Gregg 987* (MO); Tuxpán, *Viereck 1201* (US). SINALOA: Concordia, La Calera, *Trejo 1109* (US); El Habal, *González Ortega 5195* (US); Sierra Madre, Colomos, *Rose 1701* (GH, K,

NY, US); San Ignacio, *González Ortega 250* (K); Villa Unión, *Rose, Standley & Russell 13968* (GH, NY, US). WITHOUT LOCALITY: *Halsted 26* (NY), *Kerber 428* (US); *Mociño & Sessé 3784* (F), *Müller 708* (NY).

The most typical plants of this subspecies occur in the states of Morelos, Mexico, Guerrero and Michoacan, at altitudes well above 1000 m. They are characterized by a dense, soft, ferrugineous pubescence, rather small leaves, generally with five pairs of leaflets, and broad calyces; the flowers are frequently pedicellate. The material available comes from restricted and widely separate areas in the dissected slopes of the plateaus south of the Central Valley of Mexico. Its variability may be the result of geographic isolation or perhaps the influence of other species, as suggested by some aberrant specimens from an isolated locality in Jalisco (*Mexia 1842*).

Towards the north, on the western slopes of the Sierra Madre Occidental, the plants of Nayarit, Jalisco and Sinaloa are less typical, and some of them approach subsp. *vera* in many characters. The leaflets are small, elliptic to lanceolate-ovate or even obovate in the upper pair, the calyces longer than in the typical plants, and the pubescence less dense and ferrugineous. Some of these more glabrous plants with ovate leaflets have been called *I. oophylla.* It is interesting to note that in this area the genus reaches its most northern point, in the Sierra de Tres Picos, Durango; on the eastern side of the country this species reaches almost the same latitude in Coahuila, while it is not found in the intermediate areas, the vast and dry bolsons of northern Mexico.

45c. INGA VERA Willd. subsp. **SPURIA** (Willd.) J. León, stat. nov.

I. spuria Willd. in L., Sp. Pl. **4:** 1011, 1806. (ex char.; Type *Humboldt & Bonpland s.n.* photo)
Mimosa spuria (Willd.) Poir. in Lam., Encycl. Suppl. **1:** 40, 1810.
I. berteriana DC., Mém. Leg. 438, 1825 (*fide* Bentham). (Type *Bertero s.n.* photo)
I. mociniana G. Don, Gen. Syst. Pl. **2:** 388, 1832 (*fide* Bentham). (Type *Mociño s.n.*, not seen)
I. xalapensis Benth. in Hook., Lond. Jour. Bot. **4:** 616, 1845. (Type *Linden 671* photo)
Feuilleea spuria (Willd.) O. Ktze., Rev. Gen. Pl. **1:** 189, 1891.
F. xalapensis (Benth.) O. Ktze., loc. cit.
Inga donnell-smithii Pittier, Contr. U. S. Nat. Herb. **18:** 211, 1916. (Type *J. D. Smith 2316*)
I. fissicalyx Pittier, loc. cit. 213. (Type *C. A. Purpus 1917*)

Trees; branchlets terete or angulate, cinereous to ferrugineous-tomentose, lenticellate. *Leaves* with 5-9 (generally 6-7) pairs of leaflets; leaflets subcoriaceous, elliptic to lanceolate, obtuse to acuminate at the apex, rounded to obtuse at the base, above grayish when dry, sparsely pilose to scabrous, the nerves slightly prominent, beneath tomentose to glabrate, the prominent nerves more pubescent, the upper pair elliptic to falciform, 9-17 cm long, 3-4 cm wide, the basal pair lanceolate or ovate, about half to two thirds the size of the upper pair, the petiolules conic, 1-2 mm long, pilose; rhachis winged, 8-13 cm long, tomentose on the midrib, the wings cuneate, the glands small, patelliform, 1-2 mm in diam; petiole terete or winged, 0.5-1.5 cm long, tomentose, the pulvinus very short to obsolete; stipules lanceolate,

4-7 mm long, caducous. *Inflorescences* terminal or axillary, 1 to many spikes, fasciculate or paniculate; peduncle terete, slender, 4-7 cm long, tomentose; rhachis up to 5 cm long, the bracts lanceolate, 6-9 mm long, caducous. *Flowers* sessile to markedly pedicellate, the pedicels obsolete to 8 mm long; calyx turbinate, 11-19 mm long, cinereous to ferrugineous-pubescent, the teeth acute, 5-6 mm long; corolla tubular, flaring above, 15-22 mm long, the lobes obtuse, 4-6 mm long; staminal tube generally included. *Legume* sulcate when young, in age subtetragonal, the valves narrower than the margins, 8-30 cm long, 1-2 cm wide, densely cinereous or ferrugineous-tomentose.

Mexico (Guerrero and Coahuila) to Panama. (South America.)

Vernacular names: *acotope* (Veracruz–Ll. Williams); *cuje, shalun* (Guatemala–Standley & Steyermark); *guabo* (Central America).

Mexico: chiapas: Chicomucelo, *Matuda 4477* (NY); Escuintla, *Matuda 22* (MO, NY, US); Escuintla, Esperanza, *Matuda 17640* (F); Monserrate, *C. A. Purpus 10311* (NY, US); Río Usumacinta, *Reko 4131* (US). coahuila: Gómez Farías, *Palmer 290* (F, GH, MO, NY, US). hidalgo: Huejutla, *Moore 2905* (GH), *Seler 894* (GH, US). oaxaca: Cuyamecalco, *Conzatti 3487* (US); Puerto Angel to Pochutla, *Nelson 2461* (GH, US); Rincon Antonio, *Orcutt 3228* (F, GH, MO, US); San Juan Lalana, *Schultes & Reko 792* (GH); Tuxitán, Tapana, *Seler 2044* (GH); Ubero, *Ll. Williams 9186* (F, MO, US); Yaveo, Choapam, *Mexia 9288* (F, GH, MO, NY). san luis potosi: Labra, Ciudad del Maíz, *Seler 765* (GH); Micos Falls, *Vines 3329* (US); Tamasopo, Cañon, *Pringle 5045* (GH); Valles, *Fisher 3361* (F, NY). tabasco: Achotal, Balancán, *Matuda 3038* (F, NY); San Juan Bautista, *Rovirosa 27* (US). tamaulipas: Tampico, *Palmer 568* (GH, MO, NY, US); Río Sabinas, *Meyer & Rogers 2850* (MO). veracruz: Cabrestos, *Liebmann 4429* (F); Colipa, *Liebmann 4442* (F, GH, US); Córdoba, *Bourgeau 2040* (GH, US); Dos Ríos, *Mell 556* (NY, US); Fortuño, *Ll. Williams 8515* (F), *8824* (F, MO, US), *8948* (F, MO, NY, US); Jalapa, *Schiede 673* (GH, NY); Lake Catemaco, *Nelson 425* (NY, US); Orizaba, *Bilimek 127* (GH), *Müller 2208* (NY); Pánuco, *Palmer 362* (F, GH, MO, NY, US); Río de los Pescados, *C. A. Purpus 10700a* (MO, NY, US), *11110* (MO, NY); San Francisco, near Veracruz, *C. L. Smith 1401* (EAP, NY); Santa Lucrecia, *C. L. Smith 991* (EAP, GH, MO, NY, US); Tantoyuca, *Ervenberg 10* (GH); Zacualpán, *Purpus 1917* (F, GH, MO), *8625* (GH, MO, NY, US).

British Honduras: El Cayo, *Bartlett 12992* (F, NY, US); Hope Creek, *Schipp 135* (F, GH, MO, NY, US); Little Cocquericot, *Lundell 4402* (US); Manatee Lagoon, *Peck 374* (GH, K); Maskall, *Gentle 1282* (F, GH, MO, NY); Middlessex, *Schipp 293* (GH), *295* (F, MO, NY, US); Mussell Creek, east of Boomtown, *O'Neill 8601* (F, GH, NY, US); Silk Grass Reserve, *Record 18* (NY, US); Vaca, El Cayo, *Gentle 2536* (F, MO).

Guatemala: alta verapaz: Gubilgüitz, *Tuerckheim 7854* (GH, MO, NY); Semococh, *Steyermark 45732* (F); Transvaal, *C. L. Wilson 304* (F); without locality, *Brigham s. n.* (GH), *Watson 213* (GH), *343* (GH). escuintla: Iztapa, *J. R. Johnston 1168* (F); Río Guacalate, NW of Escuintla, *Standley 89294* (F); Río Michatoya, SE of Escuintla, *Standley 89200* (F); Río Michatoya, *Standley 89202* (F); San Juan Mixtán, *J. D. Smith 2317* (GH, US); San Vicente Osuna, *Tonduz & Rojas 48* (US). guatemala: Amatitlán, *Kellermann 5058* (F), *6374* (F); Chinautla, *Holway 486* (US); Guarda Viejo, *J. D. Smith 2316* (GH, US). huehuetenango: Ciénega de Lagartero, Miramar, *Steyermark 51550* (F). izabal: Boca del Cahabón, *J. D. Smith 1673* (GH, NY, US); Golfete, *Rowlee & Rowlee 308* (NY, US); Los Amates de Quiriguá, *Steyermark 38327* (F); Quiriguá, *Standley 23842* (GH, MO, US), *24507* (GH, NY), *24557* (GH, MO, US), *72248* (F), *72314* (F), Río Izabal, *Blake 7843* (US). jalapa: Cerro Alcoba, Jalapa, *Steyermark 32607* (F); Jalapa, *Standley 76751* (F). jutiapa: Jutiapa, *Standley 75643* (F); Laguna dé Ayarza, *Heyde & Lux 3727* (GH, US); Trapiche Vargas to Asunción Mita, *Steyermark 31793* (F). quezaltenango: Río Ocosito, *J. D. Smith 2822* (US). peten: El Paso, *Lundell 1505* (F, GH, MO, NY, US); Tikal, *Bartlett 12650* (F). retalhuleu: Retalhuleu, *Bernouilli & Cario 1243* (K), *Standley 66712* (F), *88666* (F), *88724* (F), *88784* (F, MO); Río Ocosito, W of Retalhuleu, *Standley 88258* (F); Río Vil, W of Retalhuleu, *Standley 88300* (F), *88328* (F). sacatepequez: without locality, *Rojas 348* (US). santa rosa: Chiquimulilla, *Standley 79177* (F); Río de Los

Esclavos, *Heyde & Lux 3290* (GH, US). SOLOLA: Patahul, *Kellermann 5883* (US). SUCHITEPEQUEZ: Alotenango, S of Tiquisate, *Steyermark 47803* (F); Sto. Domingo, S of Mazatenango, *Standley 88898* (F). ZACAPA: Gualán, *Deam 380* (GH, MO, NY, US), *6303* (GH, US); Rio Teculután, *Steyermark 42136* (F). WITHOUT LOCALITY: *Lewton 401* (US).

SALVADOR: AHUACHAPAN: Ahuachapán, *Standley 20029* (GH, MO, NY, US). CABANAS: San Nicolás, *Calderón 1587* (US). LA LIBERTAD: La Libertad, *Standley 23236* (F, GH, MO, US). LA UNION: Laguna de Maquigüe, *Standley 20935* (GH, US); Zacatecoluca, *Calderón 319* (GH, MO, NY). SAN MIGUEL: San Miguel, *Standley 21142* (GH, MO, US). SAN SALVADOR: San Martín, *Calderón 1897* (GH, US); San Salvador, *Calderón 1565* (NY, US), *Standley 22466* (GH, US); San Salvador-La Palma, *Carlson 585* (F). SAN VICENTE: San Vicente, *Standley 21228* (GH, US), *21674* (GH, US), *Standley & Padilla 3660* (F). SANTA ANA: Metapán, *Standley & Padilla 3101* (F); San Miguel de Metapán, *Carlson 765* (F), *847* (F). SONSONATE: Acajutla, *Standley 21931* (GH, US); Izalco, *Pittier 1928* (US); Nahulingo, *Standley 22047* (GH, US); San Antonio del Monte, *Standley 22151* (GH, US). WITHOUT LOCALITY: *Calderón 68* (F).

HONDURAS: ATLANTIDA: Salado, *Yuncker, Koepper & Wagner 8333* (F, GH, MO, NY, US); Tela. *Blake 7273* (US), *Standley 54718* (F, US), *55146* (F, NY, US). COMAYAGUA: Comayagua, *Standley & Chacón 5750* (F), *5936* (F); El Banco, *Valerio 2508* (F); Las Limas, *Edwards 100* (F), *337* (F, US); Río Chiquito, *Standley & Chacón 5221* (F); Rio Selán, *Valerio 2844* (F); Rio Selguapa, *Valerio 2563* (F); Siguatepeque, *Allen 6191* (EAP), *Edwards 587* (F, US), *Standley 55950* (F, US), *Standley & Chacón 6101* (F), *6710* (F), *Valerio 2673* (F), *Yuncker, Dawson & Youse 5529* (F, GH, MO). CHOLUTECA: Río Pespire, *Williams & Molina 15563* (F). EL PARAISO: Güinope, *Williams & Molina 11528* (F, GH, MO), *Williams, Molina & Padilla 2079* (F). ISLAS DE LA BAHIA: Roatán, *Gaumer 87* (K). MORAZAN: Caparrosa River, *Standley 20538* (F), *Williams & Molina 11148* (F), *11887* F, GH, MO), *12711* (F, GH); Jicarito, *Standley 21066* (EAP, F), *Williams & Molina 4027* (F); Jicarito River, *Glassman 1695* (EAP, F); Las Mesas, *Molina 312* (F); Monte de la Flor, *von Hagen & von Hagen 1131* (F, NY); Quebrade El Horno, *Molina 831* (F); San Francisco, *Williams & Molina 12198* (F, GH); San Juan del Rancho, *Standley 14327* (F); Santa Inés, *Valerio 486* (F); Villa Nueva, *Molina 84* (F); Zamorano, *Standley 1835* (F, MO), *3993* (F), *4988* (F), *Valerio 1153* (F). OLANCHO: Juticalpa, *Standley 17631* (F). YORO: Medina, Aguan River, *Yuncker, Koepper & Wagner 8621* (F, MO, NY).

NICARAGUA: CARAZO: Jinotepe, *Standley 8521* (F). CHINANDEGA: Ameya, *Maxon, Harvey & Valentine 7183* (US); *Corinto, Greenman & Greenman 5836* (MO). CHONTALES: Juigalpa, *Standley 9300* (F); La Libertad, *Standley 9142* (F); Río San Juan, *Oersted 4416* (F). GRANADA: Granada, *Baker 114* (GH, MO, NY, US), *595* (US), *837* (US); *Oersted 4424* (F); Las Isletas, *Oersted 4418* (F). JINOTEGA: Jinotega, *Standley 9692* (F). MANAGUA: Managua, *Garnier 59* (F), *4153* (F), *4182* (F). RIVAS: San Juan del Sur, *Torrey 5* (NY). ZELAYA: Braggman's Bluff, *Englesing 226* (F); Escondido River, *Long 180* (F); La Esperanza, Río Grande, *Molina 2123* (F). WITHOUT LOCALITY: *C. Wright s. n.* (GH, US).

COSTA RICA: ALAJUELA: Carrilos de Poás, *Brenes 20471* (F); Coyolar, *Standley 39987* (US), *40055* (US), *Wercklé s. n.* (US); Zarcero, *L. O. Williams 16564* (IAIAS). CARTAGO: La Carpintera, *Echeverria 404* (F), *Stork 2111* (F). GUANACASTE: Bebedero, *Brenes 12556* (F); Nicoya, *Tonduz 13855* (CR, GH, K, NY, US); Salinas Bay, *Pittier 2726* (CR, US); without locality, *Oersted 4423* (F). HEREDIA: Echeverría, *Pittier & Tonduz 2515* (CR, US); Rio Virila, *L. O. Williams 16047* (EAP, IAIAS). PUNTARENAS: Buenos Aires, *Tonduz 4988* (CR, US); Cascajal, *Holm & Iltis 220* (F); Pan de Azúcar, *León 1236* (CR); Río Ceibo, *Tonduz 3829* (CR). SAN JOSE: Alajuelita, *Echeverria 607* (CR, F); Desamparados, *Biolley 1018* (CR, US); El General, *Skutch 4695* (CR, F, MO, NY, US); Escazú, *Standley 32340* (US); La Uruca, *Pittier 358* (CR); La Verbena, *Tonduz 9078* (CR, US); Las Pavas, *Standley 36053* (US), *36072* (US); Río Tiribí, *Pittier 4258* (CR); San Francisco de Guadalupe, *Tonduz 8049* (US); San José, *Biolley 56* (F), *Greenman & Greenman 5505* (MO), *Standley 34817* (US), *39002* (US), *39008* (US); San Sebastián, *Standley 32696* (US), *49287* (NY, US). WITHOUT LOCALITY: *Oersted 14* (GH).

PANAMA: CANAL ZONE: Chiva-Chiva trail, *Maxon & Harvey 6581* (US), *Piper 5752* (US); Gatún, *Hayes 78* (GH), *258* (NY); Río Agua Salud, near Frijoles, *Piper 5866* (F, US); sabana of Panama, *Pittier 2538* (GH, NY, US); Trinidad River, *Pittier 3973* (F, GH, NY, US); Victoria Fill, *Allen 1704* (GH, NY, US). COCLE: LaPintada, *Allen 518* (GH, MO); Penonomé, *R. S. Williams 137* (NY, US), *334* (NY, US). CHIRIQUI: Boquete,

Davidson 823 (F, MO). HERRERA: Ocú, *Allen 4069* (MO). PANAMA: Chepo, *Hunter & Allen 89* (F, GH, MO), *Klug 16* (F, US); Juan Díaz, *Allen 939* (F, GH, MO, US); Las Lajas, *Allen 1608* (GH, MO, NY, US); Las Sabanas, *Bro. Paul 178* (US); Las Sabanas to Matías Hernández, *Standley 31825* (NY, US), *31871* (US), *31889* (US); San José Island, *I. M. Johnston 630* (GH), *698* (GH), *1277* (GH); Monte Oscuro, *Zetek 349* (F). VERAGUAS Cañazas, *Allen 160* (MO, US). WITHOUT LOCALITY: *Seeman 520* (GH), *Hayes 1027* (NY, US).

A subspecific value is assigned here to *I. spuria* Willd. after comparing many specimens from Central and South America with the Antillean plants. (On the type sheet of *I. spuria* at Berlin, Urban wrote: "Ab *I. vera* Willd. certes non diversa"). As no important characters were found to separate the two entities, I follow an old idea of Bentham, who considered *vera, spuria,* and probably the *uraguensis* (which I did not examine) as subspecific concepts of a widely spread species, since intergradations occur in all directions and quite often morphological types that tend to have a local distribution, reappear isolated in other regions. *Inga eriocarpa,* for instance, has been reported from Colombia, *I. vera* from Guatemala, etc.

In southeastern Mexico, British Honduras and Guatemala, an interesting variant occurs that Pittier named *I. fissicalyx;* it appears also in Costa Rica and Panama. It is characterized by long calyces that often exceed the corolla, long peduncles and narrow, lanceolate, or falciform leaflets. The extreme of this entity is represented by *Liebmann 4442* from Colipa, Veracruz. In Mexico it intergrades gradually towards other types and in Guatemala towards a peculiar type of the highlands, *I. donnell-smithii* Pittier, characterized for its ferrugineous-tomentose calyces; similar forms occur in Honduras, Costa Rica and Colombia (*I. eriocarpoides* Britton & Killip). In southern Costa Rica and Panama some plants have pedicellate flowers, as was reported for the type of *I. spuria.*

46. INGA INGOIDES (Rich.) Willd. in L., Sp. Pl. **4:** 1012, 1806. (ex char.)

Mimosa ingoides Rich., Act. Soc. Hist. Paris **1:** 113, 1792. (Type *Le Blond s.n.,* not seen)
Inga merianae Splitg., Pl. Nov. Sur. 19, 1842 (*fide* Bentham). (Type *Splitgerber s.n.,* not seen)
I. galibica Duchass. & Walp., Linnaea **23:** 747, 1850. (ex char.; Type *Duchassaing 488,* not seen)
Feuilleea ingoides (Rich.) O. Ktze., Rev. Gen. Pl. **1:** 188, 1891.

Trees up to 22 m tall; branchlets terete or angulate, ferrugineous-tomentose to glabrate, lenticellate. *Leaves* with 3-5 (generally 3) pairs of leaflets; leaflets subcoriaceous, elliptic to lanceolate, rufescent when dry, the apex obtuse to acuminate, the base rounded, above dark, lustrous, pilose to glabrescent, the nerves slightly prominent and densely pilose, beneath paler, sparsely to densely pilose, the nerves very prominent, the upper pair obovate to cuneate-elliptic, 10-22 cm long, 6-9 cm wide, the lower pair elliptic to lanceolate, 3-7 cm long, 2-3 cm wide, the petiolules conic, 1-2 mm long, densely ferrugineous-tomentose; rhachis winged, 5-12 cm long, densely tomentose on the midrib, the wings well developed, cuneate or elliptic, the glands small, patelliform, less than 1 mm in diam; petiole terete, 1.5-2.5 cm long, densely ferrugineous-tomentose, the pulvinus darker; stipules elliptic, up to 7 mm long, glabrate, caducous. *Inflorescences* 1-4 corymbiform racemes, axillary

or terminal; peduncle terete, slender, 2-8 cm long, ferrugineous-tomentose; rhachis irregular, sometimes thick, constricted, 1.5-3.0 cm long, the bracts ovate, about 2 mm long, caducous. *Flowers* markedly pedicellate, the pedicels 3-8 mm long, 1 mm in diam; calyx campanulate, 5-9 mm long, 4-5 mm wide, densely ferrugineous-tomentose, the teeth regular, obtuse to acute, 1-2 mm long; corolla tubular, deeply lobed, 10-16 mm long, appressed-pilose, the lobes obtuse, 4-5 mm long; staminal tube included, the filaments about 3 cm long; ovary oblong, sulcate, about 5 mm long, the style longer than the filaments. *Legume* terete, deeply sulcate when young, the marginal sides twice as broad as the valves, 12-35 cm long, densely ferrugineous-tomentose; seeds oblong, 1.0-1.5 cm long, 0.5 cm wide.

Guadeloupe to Trinidad. (South America, from Peru to the Guianas.)

Vernacular names: *pois-doux poilu* (Guadeloupe–Duss); *pois-doux marron* (Dominica–Beard); *pois-doux gris* (Martinique–Duss); *cacolie* (St. Lucia–Beard).

GUADELOUPE: Matouba, Camp Jacob, *Duss 3035* (NY, US); Morne Boucanier, *Duss 3229* (NY, US), *3601* (NY, US).

DOMINICA: Bellevue, *Eggers 644* (GH); Laudat, *J. S. Beard 654* (MO); Layou, *W. H. Hodge 610* (NY); Lisdora Estate, *G. P. Cooper III. 183* (GH, NY); Rosalie Valley, *Lloyd 707* (NY); Soufriere, *Eggers 110* (US); without locality, *Imray s. n.* (GH).

MARTINQUE: Case Pilote, *Duss 1158* (NY); Lamantin, *Hahn 665* (GH).

ST. LUCIA: Grand Magazin, *P. Beard 1138* (GH, MO).

ST. VINCENT: Calvary, *Eggers 6818* (US).

TRINIDAD: Arena Gov. Forest, *Broadway s. n.* (F); *5857* (MO); Arima, *Eggers & Rensch s. n.* (US); Godineau River, *Britton 2919* (GH); La Brea, *Broadway s. n.* (GH); Maqueripe, *Britton, Britton & Hazen 192* (GH, US); Port-of-Spain. *Kuntze 899* (F, NY); St. Ann, *Broadway 5116* (F, MO); Tabaquite, *Broadway 9103* (MO); without locality, *Sieber distr. 171* (GH, MO), *Trin. Bot. Gard. s. n.* (US), *2842* (US).

Inga ingoides has a wide distribution in South America and may have reached the Lesser Antilles through Venezuela via Margarita Island. It is closely related to *I. vera* and *I. edulis,* and some few collections show certain intergrading between these species and the first. Many of the specimens attributed to *I. vera* have pedicellate flowers but lack the short, campanulate calyx and large leaves of *I. ingoides.*

47. INGA COCLENSIS Pittier, Contr. U. S. Nat. Herb. **18:** 211, 1916. (Type *R. S. Williams 405*)

Trees; branchlets terete, striate, densely ferrugineous-tomentose. *Leaves* with 4-8 pairs of leaflets; leaflets elliptic to lanceolate, the apex long-acuminate, the base obtuse to rounded, above lustrous, shortly and sparsely pilose, the nerves impressed and more pubescent, beneath densely pubescent, the hairs yellow, short and curved, the nerves very prominent, the upper pair lanceolate-elliptic, often asymmetric, 9-21 cm long, 2.5-8.5 cm wide, the basal pair lanceolate, 4-8 cm long, 3-5 cm wide, the petiolules conspicuous, terete, up to 5 mm long, tomentose to glabrescent; rhachis terete, stout, 17-29 cm long, densely ferrugineous-tomentose, the glands shortly stipitate, crateriform, up to 2 mm in diam, the rim glabrous; petiole terete, thicker at the pulvinar section, 2-4 cm long, tomentose to glabrescent; the stipules minute, ovate, less than 2 mm long, pubescent, deciduous. *Inflorescences* axillary or terminal, solitary or in groups of 2-3; peduncle terete, 3.0-3.5 cm long, tomentose; rhachis 2-6 cm long, the bracts minute, ovate, 1-2 mm long,

subpersistent. *Flowers* sessile, subcongested; calyx cupulate, 4-6 mm long, shortly lanose, the teeth obtuse, about 1 mm long, more pubescent; corolla tubular, 11-15 mm long, appressed-lanose, the lobes acute, 2-3 mm long; staminal tube slightly exserted. *Legume* subterete, straight or twisted, at maturity about 35 cm long, 2.5 cm in diam, densely ferrugineous-tomentose, the margins wider than the valves.

Atlantic lowlands, from Guatemala to Panama.

Vernacular names: *nacaspiro, cuje* (Guatemala–Standley).

GUATEMALA: IZABAL: Entre Ríos, *Standley 72586* (F, NY); Milla 49.5 to Cristina, *Steyermark 38392* (F); Puerto Barrios, *Standley 73048* (F), *73078* (F).
HONDURAS: ATLANTIDA: Tela, *Standley 54269* (F, US).
NICARAGUA: ZELAYA: Bluefields, Río Escondido, *Molina 1785* (F, GH).
PANAMA: CANAL ZONE: Barro Colorado Island, *Bangham 528* (F). COCLE: Bismarck, above Penonomé, *R. S. Williams 405* (NY, US).

Inga coclensis was described by Pittier from a detached branchlet with young fruits and associated by him, on the structure of the leaf rhachis, with *I. rubiginosa* DC. of South America and *I. eriorhachis* Harms of Costa Rica. At present it is impossible to see any close relationship uniting the three species and *I. coclensis* seems to have no strong affinities among the ser. INGA. The present description is thus based on Nicaraguan and Guatemalan material for the inflorescences and the legume characters observed in the Panamanian specimens. The former do not agree completely with the type but more closely with the Bangham collection. The apparent discontinuity in Costa Rica is noteworthy. This, and some slight morphological differences, suggests the possibility of two different species, one in northern Central America and the other in Panama. The material available does not justify this separation.

SECTION III. LEPTINGA Benth. in Hook., Lond. Jour. Bot. **4:** 579, 1845.

§ *Diadema* Benth. in Hook., loc. cit. 583.

Trees; leaves large or small, glabrous or pubescent. *Inflorescences* shortly to long-pedunculate, the peduncle stout or slender. *Flowers* sessile or pedicellate, congested, the rhachis spheric or clavate, giving a capituliform or umbelliform appearance to the inflorescence. *Legume* flat.

Section LEPTINGA is formed by group of species that have in common the type of floral arrangement but in other characters do not seem to be clearly related. It is probably that the congestion of the floral racemes was attained in different groups in the genus, and that the present section is of polyphyletic origin.

SPECIES . . . 48-56

a. Calyx tubular, the teeth shorter than the tube; leaves and inflorescences not ferrugineous-setose; inflorescences on the young branchlets.
  b. Rhachis of the leaves winged or widely marginate.
    c. Calyx less than 5 mm long.
      d. Flowers with long and slender pedicels. Panama ....48. I. UMBELLIFERA
      dd. Flowers almost sessile, or the pedicels less than 1 mm long. Panama ....49. I. ALLENII
    cc. Calyx 20-25 mm long. Costa Rica and Panama ....50. I. PORTOBELLENSIS

bb. Rhachis of the leaves terete.
 e. Branchlets, inflorescences, and fruits tomentose. Mexico to Panama ....51. I. QUATERNATA
 ee. Branchlets, inflorescences, and fruits glabrous or slightly puberulous.
  f. Flowers markedly pedicellate, the pedicels 4-14 mm. long; leaves with 1-2 (rarely 3) pairs of leaflets; legume less than 15 cm long. Panama; Trinidad ....52. I. HETEROPHYLLA
  ff. Flowers sessile or very shortly pedicellate, the pedicels less than 3 mm long; leaves generally with 3-5 pairs of leaflets; legume more than 15 cm long.
   g. Stipules large, persistent, 15-20 mm long; pedicels up to 3 mm long. Mexico to Costa Rica ....53. I. PATERNO
   gg. Stipules short, caducous, up to 8 mm long; flowers sessile.
    h. Calyx 4-5 mm long; corolla pilose, often deeply cleft to one side. Costa Rica ....54. I. MORTONIANA
    hh. Calyx 1-3 mm long; corolla glabrous, regular. Mexico ....55. I. JINICUIL

aa. Calyx turbinate, the teeth longer than the tube; leaves and fruits ferrugineous-setose; flowers often in the old wood. Panama ....56. I. SAFFORDIANA

48. INGA UMBELLIFERA (Vahl) Steud., Bot. Nom. Phan. 431, 1821.

Mimosa umbellifera Vahl, Eclog. **3**: 30, 1807. (Type *von Rohr s.n.* photo)
Inga sciadion Steud., Flora **26**: 758, 1843. (Type *Hostmann & Kappler 170*)
I. umbratica Poeppig, Nov. Gen. Sp. Pl. **3**: 77, 1845. (Type *Poeppig s.n.* photo)
I. myriantha Poeppig, loc. cit. (Type *Poeppig s.n.*)
Feuilleea myriantha (Poeppig) O. Ktze., Rev. Gen. **1**: 188, 1891.
F. sciadion (Steud.) O. Ktze., loc. cit. 189.
F. umbellifera (Vahl) O. Ktze., loc. cit.
F. umbratica (Poeppig) O. Ktze., loc. cit.
Inga gracilipes Standley, Jour. Wash. Acad. Sci. **15**: 101, 1925. (Type *Standley 30353*)
I. lawrenceana Britton & Killip, Phytologia **1**: 23, 1933. (Type *Lawrence 260*)

Small *trees;* branchlets terete, shortly lanose when young, in age glabrate and densely lenticellate. *Leaves* with 2-3 pairs of leaflets; leaflets subcoriaceous, elliptic, often markedly oblique, the apex acute to acuminate, the acumen broad to triangular, the base broadly cuneate to rounded, above lustrous, glabrous, the 4-8 pairs of lateral nerves distant and prominent, the upper pair elliptic, 9-16 cm long, 4-6 cm wide, the lower pair elliptic-lanceolate, 4-6 cm long, 1-3 cm wide, the petiolules dark, 1-2 mm long, pilose or glabrous; rhachis winged, 2-11 cm long, sometimes with a linear apical appendage, the wings narrowly cuneate, broader above, becoming progressively obsolete to the base, the glands large, patelliform or subcupulate, about 2 mm in diam; petiole winged above, 1-3 cm long, glabrous or puberulent, the pulvinus black, conic; stipules linear-obovate, acute, about 5 mm long, sparsely pilose, subpersistent. *Inflorescences* axillary and solitary, or paniculate in terminal branchlets; peduncle slender, 1-5 cm long, glabrous or pilose, to woody and lenticellate; rhachis spheric, 3-4 mm long, the bracts spathulate, up to 2 mm long, pilose. *Flowers* greenish white, few to many, the pedicels slender, 7-15 mm long, sparsely pilose above; calyx cupulate-tubular, 3-5 mm long, sparsely pilose, the teeth very short and obtuse; corolla tubular-funnelform, 9-17 mm long, glabrous in the lower part, pilose at the lobes, lobes about 3 mm long; staminal tube exserted, the filaments about 1.5 cm long. *Legume* flat, oblong, 6-12 cm long, 1.5-2.5 cm wide, tomentose when young, in age glabrate.

Wet forests of the lowlands of Panama. (Brazil and Peru to the Guianas.)

Panama: canal zone: Barro Colorado Island, *Avilés 16* (F), *Bangham 488* (F), *Wood-Worth & Vestal* (F); France Field, *Standley 30353* (US).

The interpretation of variability of *I. umbellifera* is based on the study of photos of several types plus type specimens and numerous other collections from South America. The characters used in establishing some of the species here mentioned as synonyms are very unstable; they are mainly the kind of pubescence, relative length of pedicels, size of flowers, etc. Another reason for the creation of several species has been the lack of correlation between species described from the Guianas and those from Peru and Colombia. In this vast area *I. umbellifera* shows as much variability as the majority of the other South American species of *Inga*. The relation between this species and the *I. coriacea* Desv. complex is not clear at present.

49. Inga **allenii** J. León, sp. nov.

Arbor ca 15 m alta; ramulis teretibus, cortice albo. *Foliola* 3-juga elliptica apice longe acuminata acumen acuto ca 15 mm longo, basi acuta vel obtusa obliqua, supra opaca glabra minute punctata nervis lateralibus prominentibus, superiora cuneate elliptica 8-10 cm longa 3.0-3.5 cm lata, inferiora ovale elliptica 5.5-7.0 cm longa 2.5-3.0 cm lata, petiolulis brevibus ca 1 mm longis crassis glabris; rhachibus anguste alatis vel marginatis supra canaliculatis 5.0-6.5 cm longis, alis latioribus infra foliola, glandulis interfoliolaribus pyriformibus ca 3 mm longis glabris, foramine minuto albo; petiolis teretibus supra canaliculatis 2-3 cm longis glabris vel puberulis, pulvino crassiori ca 4 mm longo; stipulis oblongis ca 2 mm longis pubescentibus caducis. *Inflorescentiae* solitariae terminales vel axillares in ramulis brevibus, pedunculis gracilibus 3-4 cm longis puberulis; rhachibus globosis 3-4 mm diam; bracteis oblanceolatis 8 mm longis pilosis. *Flores* tenue pedicellati congesti; calyce tubuloso 2-3 mm long sparse piloso, dentibus inaequalibus cristatis; corolla tubulosa 6-7 mm long pilosa, lobis acutis 1.0-1.5 mm longis; tubo staminali incluso vel exserto filamentis ca 5 cm longis. *Legumen* ignota.

Panama: cocle: hills north of El Valle de Antón, trail to La Mesa, about 1000 m elev., *Allen 2687* (holotype US).

Allied to *I. mortoniana* in the structure of the leaves and inflorescence; easily separated on account of the shape of the glands and the winged rhachis.

50. Inga portobellensis Beurl., Svensk. Vet. Akad. Handl. **1854:** 122, 1856. (Type *Billberg 72*)

Inga macrophylla Billb. ex Beurl., loc. cit., pro syn., non Willd.

Trees, almost completely glabrous; branchlets terete, lenticellate. *Leaves* large, with 2 pairs of leaflets; leaflets coriaceous, obovate-oblong, the apex acute to long-acuminate, the acumen up to 2 cm long, the base acute, unequal, slightly cordate or revolute, above dark green, lustrous, except for the puberulent midnerve, the

nerves impressed, beneath paler, glabrous or sparsely pilose on the nerves and margin, the nerves prominent, the upper pair obovate-oblong to spathulate, 9-25 cm long, 6-10 cm wide, the lower pair oblong, 6-10 cm long, 3-5 cm wide; rhachis cuneately winged 5-12 cm long, with a terminal, linear, deciduous appendage up to 16 mm long and 2 mm wide, the glands shortly stipitate, hemispheric, pertuse; petiole short, 1-3 cm long, winged above, the pulvinus terete and thicker; stipules foliaceous, ovate to ovate-lanceolate, acuminate at the apex, cordate at the base, 6-18 mm long, 5-9 mm wide, solitary or in groups of 2-3, subpersistent. *Inflorescences* solitary, axillary; peduncle terete, 1-5 cm long, glabrous or puberulent, with an involucre of stipules, the bracts ovate-oblong, up to 12 mm long, caducous; rhachis spheric, about 3 mm in diam, with 8-20 flowers, the bracts spathulate 3-7 mm long, caducous. *Flowers* pedicellate, the pedicels thick, 4-5 mm long; calyx tubular-funnelform, 24-26 mm long, 10-12 mm wide, striate, glabrous except at the tips, the teeth 3 mm long, pilose; corolla tubular, 38-42 mm long, glabrous except at the tip of the lobes, the lobes 3-4 mm long, sparsely pilose; staminal tube very exserted, 40-45 mm long, the filaments about 2 cm long. *Legume* (immature) flat, oblong, curved, apiculate, about 19 cm long, 3 cm wide, the margins thick and slightly elevated.

Lowlands of Costa Rica and Panama.

COSTA RICA: PUNTARENAS: Playa Blanca, *M. Valerio 468* (CR, F); Santo Domingo de Golfo Dulce, *Tonduz 9879* (CR, GH, MO, NY, US).

PANAMA: CANAL ZONE: Río Pequení, between Salamanca and Río Boquerón, *Allen 17282* (GH, MO). COLON: Portobello, *Billberg 72* (photo, MO).

An outstanding species due to its large, glabrous flowers, globose inflorescence, and large, permanent stipules. It belongs to a group represented only in Brazil by two species: *I. cordistipula* Mart., with smaller and more numerous flowers, and *I. inflata* Ducke, especially noteworthy by its huge calyx. The Costa Rican specimens do not match Beurling's description well, especially in the size of the flowers. *Allen 17282* is a young specimen, the flowers in bud, with long and slender peduncles; it offers, however, the same type of inflorescence and leaves as the Tonduz collection.

51. INGA QUATERNATA Poeppig, Nov. Gen. Sp. Pl. **3:** 79, 1844. (ex char.)

Feuilleea quaternata (Poeppig) O. Ktze., Rev. Gen. Pl. **1:** 188, 1891.
Inga maxoniana Pittier, Contr. U. S. Nat. Herb. **18:** 174, 1916. (Type *Pittier 6012*)
I. roussoviana Pittier, loc. cit. 175. (Type *Pittier 5270*)
I. williamsii Pittier, loc. cit. 176. (Type *R. S. Williams 285*)
I. schippii Standley, Publ. Field Mus. Nat. Hist., Bot. Ser., **11:** 132, 1932. (Type *Schipp 538*)
I. santanderensis Britton & Killip, Ann. N. Y. Acad. Sci. **35:** 114, 1936. (Type *Killip & Smith 15477*)
I. mutisii Britton & Killip, loc. cit. (Type *Mutis 3644*)

Trees up to 15 m tall; branchlets terete, ferrugineous-tomentose to glabrous, lenticellate. *Leaves* with 3-4 pairs of leaflets; leaflets oblanceolate to ovate, the apex acute, truncate or ending in a short mucro, the base acute to obtuse, above lustrous and glabrous, or pubescent along the main nerves, beneath shortly pilose,

the distant nerves prominent, the upper pair narrowly oblanceolate to obovate to elliptic, 7-21 cm long, 3-7 cm wide, the lower pairs elliptic to ovate, the basal about half the size of the terminal pair, the petiolules thick, terete, 1-3 mm long; rhachis terete, 3-8 cm long, tomentose to glabrescent, the glands stipitate, disciform or patelliform, often obsolete; petiole terete, 1-3 cm long, the pulvinus conic and thicker; stipules obcordate, 1.0-1.5 mm long, tomentose, caducous. *Inflorescences* solitary and axillary, or terminal on the new shoots; peduncle terete, 2.5-3.5 cm long, densely ferrugineous-tomentose; rhachis short, clavate, 1-3 mm long, giving to the inflorescence a capituliform appearance, the bracts conspicuous, the lower ones obovate, the upper spathulate, up to 2.5 mm long, pilose outside, subpersistent. *Flowers* sessile to long pedicellate, the pedicels slender, obsolete to 9 mm long, ferrugineous-pubescent; calyx tubular to tubular-subcampanulate, 2-7 mm long, pubescent, the teeth spreading, 1.0-2.5 mm long; corolla tubular-funnelform, 5-11 mm long, appressed-pubescent, the lobes 1-2 mm long; staminal tube included or exserted. *Legume* flat, oblong, apiculate at the apex, rounded at the base, 3-18 cm long, 2-3 cm wide, about 1.5 cm thick when mature, densely ferrugineous-pubescent when young, in age glabrate or thinly pilose, the margins elevated.

Wet lowlands, from 0-600 m elev., from Mexico to Panama. (South America.)

Vernacular names: *acotopillo de montaña* (Veracruz-Ll. Williams); *guabito cansa boca* (Panama-Standley).

Mexico: veracruz: Fortuño, *Ll. Williams 8472* (F).

British Honduras: Banana Creek, Cockscomb Mts., *Schipp 538* (F, MO); Camp 31, *Schipp 1283* (F, GH, MO).

Guatemala: izabal: Quiriquá, *Standley 23954* (US), *23956* (NY, US).

Honduras: atlantida: La Ceiba, *Yuncker, Koepper & Wagner 8337* (F, GH, MO, NY, US), *8564* (F, GH, MO, NY, US); Lancetilla, *Standley 56834* (F, NY, US); Puerto Sierra, *P. Wilson 41* (NY); Tela, *Standley 56619* (F, US).

Costa Rica: cartago: Las Vueltas, Tucurrique, *Tonduz 13125* (US). puntarenas: Sto. Domingo de Golfo Dulce, *Tonduz 10032* (CR, GH, NY, US).

Panama: bocas del toro: Changuinola Valley, *Cooper & Slater 13* (F, US), *Stork 272* (US). canal zone: Barro Colorado Island, *Bangham 512* (F, US), *Bailey 270* (F, GH), *Brown 71* (F), *171* (F), *Dodge & Allen 17049* (GH), *Kenoyer 364* (US), *365* (US), *Killip 40022* (MO, US), *Shattuck 1128* (F), *Steyermark & Allen 16781* (GH), *Wetmore & Abbe 40* (F, GH), *97* (F, GH), *101* (F, GH), *Woodworth & Vestal 383* (F), *569* (F), *616* (F), *Zetek 3579* (F), *3586* (F), *3827* (F), *3929* (F, MO); France Field to Catival, *Standley 30170* (US), *30335* (US). chiriqui: San Félix, *Pittier 5270* (GH, US). cocle: Penonomé, *R. S. Williams 285* (US).

The interpretation of this species is based on Poeppig's ample description, since the type was not available for my study. *Inga quaternata* is one of the most variable species in this genus and has been the basis of indefinite segregates based on the varying shape of leaflets, length of peduncles and pedicels, type of pubescence, etc. The three characters mentioned, however, have a wide variation in the same specimen: *Pittier 5270,* for instance, has pedicels that vary from 5 to 38 mm in length. In central Panama the trend is towards smaller and rounded leaflets, short peduncles and almost sessile flowers, but there occur all intermediates; in British Honduras and Guatemala the leaflets are larger and the peduncles longer. There are all types of intergradation in South America also, such as among *I. wittiana* Harms, *I. pardoana* Harms, *I. boliviana,* Rusby, *I. conglomerata* Benoist

and *I. mathewisiana* Benth., which are probably but local variants within a wide complex.

Another problem arises in the relationship of *I. quaternata* Poeppig and *I. nobilis* Willd. The basic character to set them apart, even in different sections, is the clavate type of receptacle in the first, a definite raceme in the second. The floral bracts are alike, however, and in fruit or sterile condition they are impossible to tell apart (cf. Publ. Field Mus. Nat. Hist., Bot. Ser., **13**(3): 33, 1943). Only more collections will clarify this interesting relationship.

52. Inga heterophylla Willd. in L., Sp. Pl. **4**: 1020, 1806. (Type *Hoffmansegg s.n.* photo)

Mimosa parae Poir. in Lam., Encycl. Suppl. **1**: 44, 1810. (ex char.)
Inga umbellata G. Don, Hist. Dichl. Pl. **2**: 391, 1832. (ex char.)
I. protracta Steud., Flora **1843**: 758, 1843. (Type *Hostmann & Kappler 1194*)
Feuilleea heterophylla (Willd.) O. Ktze., Rev. Gen. Pl. **1**: 188, 1891.
F. stenocarpa (Spruce) O. Ktze., loc. cit. 189.
Inga mapiriensis Pittier, Contr. U. S. Nat. Herb. **18**: 174, 1916. (Type *Buchtien 1768*)

Small *trees;* branchlets terete, striate, puberulent to completely glabrous, lenticellate. *Leaves* small, in the fertile branches with 1 or rarely 2 pairs of leaflets, in the sterile branches with 3-4 pairs; leaflets subcoriaceous, ovate to lanceolate-elliptic, the apex markedly attenuate and acuminate, shortly mucronate, the base cuneate, above dark green, lustrous, glabrous, the nerves slightly prominent, beneath paler, glabrous, the nerves prominent and finely reticulate, the upper pair elliptic to lanceolate, strongly oblique, 3-8 cm long, 2.5-3.0 cm wide (apparently somewhat larger in South America), the lower pair considerably shorter, 2-5 cm, 1.0-2.5 cm wide, the petiolules terete, up to 2 mm long, glabrous; rhachis terete, obsolete to 2 cm long, glabrous, the glands minute, hemispheric, pertuse at the apex, less than 1 mm in diam; petiole terete, 0.5-1.0 cm long, the pulvinus conic and darker; stipules linear, 2-3 mm long, caducous. *Inflorescences* umbelliform, axillary on the terminal branchlets, solitary or in groups; peduncle very slender, 0.7-1.5 cm long, glabrous; rhachis spheric or clavate, 2-4 mm long, pilose to glabrous, the bracts small, triangular, caducous. *Flowers* few to many in each umbel; pedicels slender, 4-12 mm long, glabrous; calyx cupulate, 0.7-1.5 mm long, glabrous except at the tips of the segments, the teeth minute, pilose; corolla white, tubular, slender, 4.5-6.0 mm long, glabrous, the lobes spreading, 1-2 mm long; staminal tube included to slightly exserted, the filaments about 1 cm long. *Legume* flat, oblong, straight or curved, apiculate, stipitate, 7-14 cm long, 1-2 wide, glabrous, the margins slightly prominent.

Lowland forests and bushlands of Trinidad and Panama. (Northern South America, Peru and Brazil, sometimes in xerophytic habitats.)

Panama: coclé: Bismarck, above Penonomé, *R. S. Williams 600* (NY).
Trinidad: Aripo, road via Arima, *Broadway 5839* (MO); woods at Omora, *Eggers 1416* (US); without locality, *Herb. Bot. Gard. Trin. 1032* (US).

This is a remarkable species allied to a South American complex including *I. tarapotensis* Benth., *I. lateriflora* Miquel, *I. panuriensis* Benth., etc. The Panamanian

plant, referred previously to *I. laurina* (Sw.) Willd. (= *I. fagifolia*) was first attributed to *I. heterophylla* by Schery (Ann. Missouri Bot. Gard. **37:** 194, 1950). It is a mature specimen, in fruit, slightly different from the South American specimens in foliage characters, but the stipitate fruit and spheric receptacle ally it undoubtedly to *I. heterophylla.*

53. Inga paterno Harms in Fedde, Rep. Sp. Nov. **13:** 419, 1914. (ex ic.; Type *Preuss 1387*) [cf. Preuss, Exp. Central- und Sudamer. *pl. 8, fig. 6, pl. 9,* 1901]

I. radians Pittier, Contr. U. S. Nat. Herb. **18:** 178, 1916. (Type *Cook 805*)

Trees 8 to 15 m tall; branchlets terete or costate, glabrous, lenticellate. *Leaves* with 3-5 (generally 4) pairs of leaflets; leaflets coriaceous, obovate to lanceolate, the apex acute to long-acuminate, the base acute to rounded, sometimes decurrent, above lustrous, glabrous, the 5-8 pairs of lateral nerves prominent, beneath paler, glabrous, the nervation conspicuous, the upper pair elliptic to obovate, 7-18 cm long, 3-7 cm wide, the basal pair lanceolate-oblong to obovate, 6-10 cm long, 3-4 cm wide, the petiolules conic, canaliculate, 4-6 mm long, pilose, rhachis terete or slightly angulate, sometimes with margins in the upper sections, 8-16 cm long, glabrous to sparsely pilose, ending in a filiform appendix, up to 11 mm long, the glands cupuliform, sessile or stipitate, very often obsolete; petiole terete, 1.5-3.0 cm long, glabrous to sparsely pilose, the pulvinar section thicker and darker; stipules obovate to oblong, rounded or obtuse at the apex, 10-20 mm long, striate, glabrous, persistent. *Inflorescences* axillary, paniculate on short branches, or solitary; peduncle slender, 2-8 cm long, striate, sparsely pilose to glabrescent; rhachis spheric, 3-5 mm in diam, the bracts spathulate, 1 mm long, pilose. *Flowers* congested in umbelliform inflorescences, with pedicels from 0.5-3.0 mm long; calyx tubular, 1.5-2.0 mm long, glabrous or very sparsely pilose, the teeth acute, 0.5 mm long, tufted; corolla tubular to slightly funnelform, 4.0-7.5 mm long, glabrous to sparsely pilose, the lobes acute to obtuse, 1-2 mm long, tufted; staminal tube included or exserted, the filaments 0.5-1.0 cm long. *Legume* flat, depressed between the seeds, up to 40 cm long, 7 cm wide and 3 cm thick, transversely striate, glabrous, the margins elevated; seeds oblong, 5 cm long, 2 cm wide, covered by thick, white, and succulent aril.

Mexico to Salvador; cultivated in Honduras and Costa Rica.

Vernacular names: *cuil machetón* (Oaxaca); *paterno* (Guatemala, Salvador, Costa Rica); *guabo caite* (Costa Rica).

Mexico: chiapas: Acacoyagua, Escuintla, *Matuda 16496* (EAP, F); Monte Ovando, *Matuda 2075* (F); Tapachula, *Cook 805* (US); oaxaca: Concordia, *Morton & Makrinius 2414* (F, US), *2528* (F, US); Oaxaca, *Conzatti & González 1146* (GH), *Nelson 349* (US); San Andres Tuxtla, *Nelson 487* (US); Talea, *Galeotti 1* (F). veracruz: Chinameca, *Orcutt 3279* (F).

Guatemala: alta verapaz: Cobán, *Standley 91215* (F), *91218* (F); *91304* (F); El Tambor, *Tejada 339* (US); Sepacuité, *Cook & Griggs 42* (US), *100* (US), *655* (US), *783* (US). escuintla: Escuintla, *J. D. Smith 2820* (US). el progreso: Piamonte, *Steyermark 43746* (F). el quiche: San Miguel Uspatán, *Heyde & Lux 3309* (GH, US). guatemala: Chinantla, *J. D. Smith 2819* (GH, US). peten: La Libertad, *Aguilar 377* (F, MO). quezaltenango: Finca Pirineos, *Steyermark 33398* (F). san marcos: El Porvenir, *Steyer-*

mark 37189 (F). SANTA ROSA: Barberena, *Hedye & Lux 3280* (GH, US); Cuajiniquilapa, *Heyde & Lux 6122* (GH, NY, US). SUCHITEPEQUEZ: Cocales, *Standley 62069* (F).

SALVADOR: LA LIBERTAD: Sta. Tecla, *Lévy 787* (EAP). SAN SALVADOR: San Salvador, *Calderón 1641* (US), 283 (GH, NY, US), *284* (F, GH, MO, NY, US), *1642* (US), *Standley 21756* (F, GH, MO, NY, US), *23563* (GH, NY, US). SONSONATE: Sonsonate, *Standley 22326* (GH, US).

HONDURAS: COMAYAGUA: Siguatepeque, *Standley & Chacón 6664* (F). EL PARAISO: Güinope, *Williams & Molina 9032* (GH, F).

NICARAGUA: MANAGUA: Sierra de Managua, *Uribe 434* (US).

COSTA RICA: ALAJUELA: Alajuela, *J. D. Smith 6490* (US). CARTAGO: Cartago, *Torres 96* (F), *97* (F); Turrialba, *Holdridge 2556* (IAIAS), *León 2792* (IAIAS). SAN JOSE: Escazú, *Solís 186* (CR, F, MO), *289* (CR, F, MO); San José, *Cook & Doyle 15* (US).

Pittier discusses this species at length (Contr. U. S. Nat. Herb. **18:** 178, 1916) and divides it into two: *I. paterno* Harms which he restricts to the highlands of Guatemala and Costa Rica, and *I. radians* found in the Pacific lowlands of Guatemala, Chiapas and Oaxaca. The separation is based on legume characters, established probably on abnormal fruits which are frequently due to the malformation of seeds. In the other characters used by Pittier there are intermediates that also invalidate the separation.

There is a close relationship between *I. paterno* and *I. jinicuil*, if indeed they are not the same species. But with the available specimens it is inadvisable to join them since they differ constantly in size and persistency of the stipules, size and shape of the calyx, and number and shape of the leaflets. It is quite probable that this separation will disappear once more when collections are made in Chiapas, Veracruz, and Oaxaca.

Inga paterno is the only Central American species that has a fruit of good quality; for this reason the center of origin is difficult to ascertain and the cultivated area extends now from Mexico to Costa Rica. It was the first *Inga* planted for shading coffee; but a high susceptibility to a kind of witches-broom disease, and the damage made to the coffee trees by people who collect legumes, is causing the abandoning of its cultivation.

54. INGA **MORTONIANA** J. León, sp. nov.—Fig. 6.

Arbor 12-15 m alta; ramulis teretibus sulcatis vel bullatis glabris vel puberulis cortice albo lenticellato. *Foliola* 3-juga subcoriacea elliptica vel lanceolato-elliptica, apice acuta, basi obtusa vel subacuta in petiolam decurrentia, supra nitida glabra nervis prominentibus, subtus palliodoria glabra nervis prominentibus sparse pilosioribus nervationi reticulato conspicuo, superiora elliptica 9-17 cm longa 4-6 cm lata, inferiora lanceolata elliptica plerumque obliqua 4.5-9.0 cm longa 2.5-4.0 cm lata, petiolulis crassis angulatis fuscis 4-6 mm longis glabris; rhachibus teretibus vel angulatis 3.5-10.0 cm longis glabris, glandulis interfoliolaribus cupuliformibus ca 1 mm altis, foramine angusto; petiolis teretibus 2-3 cm longis glabris pulvino crasso 1.0-2.5 cm longo. *Inflorescentiae* capituliformes solitariae vel geminatae plerumque axillares in ramulis lateralibus brevibus rarius terminales; pedunculis teretibus 4.0-7.5 cm longis sparse pilosis, rhachibus globosis ca 2 mm diam bracteis linearibus 2.5 mm longis pilosis deciduis. *Flores* tenue pedicellalti

Fig. 6. *Inga mortoniana* J. León

in capitulo aggregati; calyce cupulato tubuloso 5-7 mm longis tubo sparse piloso basim apicem dense piloso, dentibus obtusis plerumque inaequalibus 0.5-1.5 mm longis; corolla tubulosa supra dilatata 9-11 mm longa appresse pilosa, lobis acutis 1.5-2.5 mm longis; tubo staminali exserto filamentis ca 1 cm longis; ovarium oblongum ca. 1.5 mm longum glabrum. *Legumen* oblonga lata 12 cm longa 4 cm lata transverse striata glabra.

Cloud forests of central Costa Rica from 1100 to 1500 m elevation.

Vernacular name: *guaba-maría* (Costa Rica—A. Smith).

COSTA RICA: ALAJUELA: Buena Vista, San Carlos, *Barquero 3* (IAIAS); La Palma, San Ramón, *Brenes 5516* (F); Tapezco, Zarcero, *A. Smith 1230* (F, HOLOTYPE NY); San Luíz, Zarcero, *A. Smith 170* (NY, MO); Vara Blanca, *Skutch 3315* (MO, NY), *3763* (MO, NY), *3780* (MO); Zapote, Zarcero, *A. Smith 2894* (EAP); Zarcero, *A. Smith 459* (F, MO, US).

This remarkable species, named in honor of Mr. C. V. Morton, U. S. National Herbarium, belongs to the group of *I. paterno* and *I. jinicuil* of northern Central America, but differs from both in the length and structure of the flowers and the number and shape of the leaflets. The spheric rhachis of the inflorescence is definitely of the LEPTINGA type.

55. INGA JINICUIL Schlecht., Linnaea **12:** 559, 1838. (Type *Schiede* 675)

Trees; branchlets terete or angulate, glabrous, conspicuously lenticellate. *Leaves* with 3 pairs of leaflets; leaflets coriaceous, elliptic to lanceolate, acute to rounded, often asymmetric at the apex, the base acute to obtuse, oblique, decurrent, above lustrous, glabrous except along the pilose costa, the 5-7 pairs of lateral nerves distant and slightly prominent, the tertiary nervation conspicuous, beneath dull, glabrous, the nerves not markedly prominent, the upper pair elliptic, 8-15 cm long, 3-6 cm wide, the lower pair lanceolate-elliptic, 3-7 cm long, 1-5-3.0 cm wide, the petiolules dark conic, 2-4 cm long sparsely pilose; rhachis terete, 4-7 cm long, glabrous, lenticellate in the lower part, the glands orbicular, pedicellate or sessile, often obsolete; petiole terete, 1.5-2.0 cm long, glabrous, striate, lenticellate, the pulvinus conic and darker, 3-4 mm long; stipules oblong, 8 mm long, 3 mm wide, glabrescent, caducous. *Inflorescences* in groups of 3-7, rarely solitary, axillary generally below the new growth; peduncle slender, terete, 2-8 cm long, striate, glabrous to sparsely pubescent; rhachis globose, 3-4 mm in diam; *flowers* sessile or very shortly pedicellate, the pedicels up to 0.5 mm long; calyx campanulate, 1.0-2.5 mm long, glabrous or sparsely pubescent, the teeth short, acute, with tufts or hairs at the tips; corolla funnelform, 3-7 mm long, glabrous, the lobes 1.0-1.5 mm long, sparsely pubescent at the tips; staminal tube generally included, the filaments 6-8 mm long. *Legume* (*fide* Schiede) oblong, straight or curved, 15 cm long, 2.5 cm wide, glabrous.

Highlands of Veracruz and Michoacán, from 600 to 1200 m elevation.

Vernacular name: *jinicuil.*

MEXICO: MICHOACAN: Coahuayula, *Emrik 38* (F). VERACRUZ: Colipa, *Liebmann 4440* (F); Córdoba, *Bougeau 2043b* (GH, K); Jalapa, *Pringle 8134* (F, GH, MO, NY, US), *Schiede 675* (F, GH, MO), *C. L. Smith 1438* (EAP, NY); Orizaba, *Bilimek 137* (GH), *Mohr 1765* (US); Teocelo, *Goldman 690* (US); Zacualpán, *C. A. Purpus 6325* (F, GH, NY).

Inga jinicuil is found in cultivation in the eastern side of Mexico, especially around the Indian dwellings in Veracruz. The area of origin is unknown. The large fruits have seeds with thick and sweet arils, and are often sold in the markets. The relationship between this species and its western relative, *I. paterno,* is discussed under the last species.

56. Inga saffordiana Pittier, Contr. U. S. Nat. Herb. **18:** 176, 1916. (Type *Pittier* 5676)

Low *trees,* with long, pendant branches; branchlets terete, striate, densely setose, lenticellate. *Leaves* with 4-5 pairs of leaflets; leaflets subchartaceous, ovate to obovate-elliptic, the apex acute to acuminate, the acumen linear, ciliate, about 4 mm long, the base oblique, cuneate, above sublustrous and glabrous except at the ciliate margins, the nerves slightly prominent, beneath sparsely setose but more densely on the costa and main nerves, lateral nerves 6-9, ascending, prominent, the intercalary nervation conspicuous, the upper pair spathulate to obovate-elliptic, 7-8 cm long, 2-3 cm wide, the lower pair lanceolate, 4.5-5.0 cm long, 2.5-3.0 cm wide, the petiolules about 2 mm long, sparsely setose; rhachis terete, 16-17 cm long, striate, setose, the glands long stipitate, 2.5-3.0 mm long, glabrous, pertuse and thicker at the apex, the terminal appendix linear, about 5 mm long, ciliate; petiole terete, 2.5-3.0 cm long, striate, densely setose, the pulvinus fleshy, 4-5 mm long, lustrous; stipules subulate, 5-14 mm long, setose, persistent. *Inflorescences* globose, long-pedunculate, cauliflorous (?) or on short spurs; peduncle slender, 4-12 cm long, setose; rhachis spheric, 2-3 mm in diam, the bracts subulate, bristly, about 5 mm long, the lowermost persistent. *Flowers* long-pedicellate; calyx (persistent in the immature fruits) conic, about 12 mm long, sparsely setose, the teeth subulate, about 11 mm long; corolla tubular, dilating above, 16 mm long, very sparsely pilose, the lobes 2.5 mm long, more pubescent. *Legume* (immature) flat, oblong, apiculate at the apex, cuneate at the base, 26-33 cm long, 2.5-3.0 cm wide, densely ferrugineous-setose.

Lowlands of western Panama. (Colombia?)

Panama: darien: Cerro de Garagará Sambú basin, *Pittier 5676* (US).

This poorly known species is unique in the genus in having cauline inflorescences; this important character plus the shape of the leaves and structure of the flower, put it in a group by itself apart from any known species. Although its position within leptinga is justified by the type of inflorescence, it has some characters of the indument and structure of the calyx that recall some species of § inga (viz. ser. pilosiusculae). A Colombian collection (*A. Fernández 267*) from the Chocó, in the same general region where *I. saffordiana* was found, is the most comparable specimen seen. However it has only 2-3 pairs of leaflets and the slender, long-pedunculate inflorescences are born on the branchlets; the flower and type of indument are very similar to *I. saffordiana.*

Several South American species of *Inga* are found in cultivation at the botanic gardens and experiment stations in the West Indies, mainly in relation to their value as fruit trees or in connection to the use as shade trees for coffee and cacao.

Inga spectabilis Willd.

Cuba: santa clara: Soledad Garden, *J. G. Jack 8501* (US).

Inga fastuosa Willd.

Cuba: santa clara: Soledad Garden, *J. G. Jack 8472* (US). Puerto Rico: mayaguez: Mayagüez, *Toro 13* (NY).

Inga quaternata Poeppig.

Puerto Rico: mayaguez: Mayagüez, *Toro 11* (NY).

Excluded Species

Martens & Galeotti, (Bull. Acad. Brux. 10, **2:** 318-321, 1843) described the following species from Mexico: *Inga? sericea* Mart. & Gal. (loc. cit. 318); *I.? nitens* Mart. & Gal. (loc. cit.); *I. laevigata* Mart. & Gal. (loc. cit.); *I. speciosa* Mart. & Gal. (loc. cit. 320); and *I. elegans* Mart. & Gal., (loc. cit. 321). From the descriptions it is clear that none belong to *Inga* and probably most of them are referable to *Calliandra.*

Inga anomala Kunth, Mim. 70, 1819 = *Calliandra grandiflora* (L'Her.) Benth. in Hook., Lond. Jour. Bot. **2:** 139, 1840.

I. billbergiana Benth., in Hook., Lond. Jour. Bot. **4:** 585, 1845 = *Pithecellobium rufescens* (Benth.) Pittier, Contr. U. S. Nat. Herb. **18:** 181, 1916.

I. canescens Cham. & Schl., Linnaea **5:** 592, 1830 = *Calliandra canescens* (Cham. & Schl.) Benth. in Hook., Lond. Jour. Bot. **3:** 96, 1844.

I. cognata Schl., Linnaea **12:** 560, 1838 = *Pithecellobium cognatum* (Schl.) Benth. in Hook., Lond. Jour. Bot. **5:** 107, 1846.

Inga coriacea G. Don, Gen. Hist. Dichl. Fl. **2:** 390, 1832. (Type *Mociño & Sessé s.n.* in herb. Lamb., Mexico). The type was not available and the description is insufficient to refer it to any of the other species of *Inga* occurring in Mexico.

I. cyclocarpa (Jacq.) Willd. in L., Sp. Pl. **4:** 1026, 1806 = *Enterolobium cyclocarpum* (Jacq.) Griseb., Fl. Brit. W. Ind. 226, 1861.

I. emarginata Willd. in L., Sp. Pl. **4:** 1009, 1806 = *Calliandra emarginata* (Willd.) Benth. in Hook., Lond. Jour. Bot. **3:** 95, 1844.

I. englesingii Standl., Trop. Woods **17:** 27, 1929 = *Pithcellobium englesingii* (Standl.) Standl., Trop. Woods **34:** 40, 1933.

I. foetida (Jacq.) Willd. in L., Sp. Pl. **4:** 1008, 1806 = *Piptadenia foetida* (Jacq.) Benth., Trans. Linn. Soc. **30:** 366, 1875.

I. fragrans Macfay, Fl. Jamaica **1:** 309, 1837 = *Acacia berteriana* (Benth.) Fawc. & Rendle, Fl. Jamaica **4:** 145, 1920.

Inga gigantifoliola Schery, Ann. Missouri Bot. Gard. **37:** 218, *fig.* 83, 1950 = *Pithecellobium* GIGANTIFOLIOLUM (Schery) J. León, comb. nov. This plant undoubtedly belongs to *Pithecellobium* because of its twice-pinnate leaves. This is easily seen in the type specimen (*von Wedel 2349,* MO) and more clearly in a collection from Livingston on the Reventazón, Prov. of Limón, Costa Rica (*Rowlee & Stork 793*). Here also belongs *Tonduz 9176* from Shirores, Talamanca, Costa Rica, in the same general region as the type collection.

I. globulifera Benth. in Hook., Lond. Jour. Bot. **4:** 585, 1845 = *Pithecellobium rufescens* (Benth.) Pittier, Contr. U. S. Nat. Herb. **18:** 181, 1916.

I. guadalupensis Desv., Jour. Bot. **1:** 70, 1814 = *Pithecellobium unguis-cati* (L.) Benth. in Hook., Lond. Jour. Bot. **3:** 200, 1844.

I. guatemalensis Hook. & Arn., Bot. Beechey Voy. 419, 1841 = *Mimosa guatemalensis* (Hook. & Arn.) Benth., Bot. Voy. Sulph. 89, 1844.

I. houstoni DC., Prodr. **2:** 442, 1825 = *Calliandra houstoniana* (Mill.) Standl., Contr. U. S. Nat. Herb. **23:** 386, 1922.

I. latifolia Willd. in L., Sp. Pl. **4:** 1020, 1806 = *Pithecellobium latifolia* Willd. in L., Sp. Pl. **4:** 1020, 1806 = *Pithecellobium latifolium* (L.) Benth. in Hook., Lond. Jour. Bot. **3:** 214, 1844.

I. leucantha Presl, Bot. Bemerk. 65, 1844 = *Pithecellobium dulce* (Roxb.) Benth. in Hook., Lond. Jour. Bot. **3:** 199, 1844.

I. macrocarpa M. E. Jones, Contr. Western Bot. **15:** 140, 1929 = *Hymenaea courbaril* L., Sp. Pl. 1192, 1753.

I. membranacea Benth., Trans. Linn. Soc. **30:** 606, 1875 = *Pithecellobium membranaceum* (Benth.) Schery, Ann. Missouri Bot. Gard. **37:** 228, 1950.

I. patens Hook. & Arn., Bot. Beechey Voy. 419, 1841 = *Entada patens* (Hook. & Arn.) Standl., Contr. U. S. Herb. **23:** 349, 1922.

I. peckii Robinson, Proc. Amer. Acad. Sci. **49:** 502, 1913 = *Pithecellobium belizense* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser., **4:** 212, 1929.

I. pennatula Cham. & Schl., Linnaea **5:** 593, 1830 = *Acacia pennatula* (Cham. & Schl.) Benth. in Hook., Lond. Jour. Bot. **1:** 390, 1842.

I. pungens Willd. in L., Sp. Pl. **4:** 1044, 1806 = *Pithecellobium dulce* (Roxb.) Benth. in Hook., Lond. Jour. Bot. **3:** 199, 1844.

I. purpurea (L.) Willd. in L., Sp. Pl. **4:** 1021, 1806 = *Calliandra purpurea* (L.) Benth. in Hook., Lond. Jour. Bot. **3:** 104, 1844.

I. rufescens (Benth.) in Hook., Lond. Jour. Bot. **4:** 585, 1845 = *Pithecellobium rufescens* (Benth.) Pittier, Contr. U. S. Nat. Herb. **18:** 181, 1916.

I. saman (Jacq.) Willd. in L., Sp. Pl. **4:** 1024, 1806 = *Pithecellobium saman* (Jacq.) Benth. in Hook., Lond. Jour. Bot. **3:** 95, 1844.

I. semicordata Bertol., Fl. Guatem. 441, 1840 = *Calliandra emarginata* (H. & B.) Benth. in Hook., Lond. Jour. Bot. **3:** 95, 1844.

I. speciosa Mart. & Gal., Bull. Acad. Brux. 10, **2:** 320, 1843 = *Calliandra cumingii* Benth. in Hook., Lond. Jour. Bot. **2:** 140, 1840.

I. stevensoni Standl., Trop. Woods **23:** 7, 1930 = *Pithecellobium stevensoni* (Standl.) Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser., **23:** 164, 1944.

I. tergemina Willd. in L., Sp. Pl. **4:** 1008, 1806 = *Calliandra tergemina* (Willd.) Benth. in Hook., Lond. Jour. Bot. **3:** 96, 1844.

I. tetraphylla G. Don, Hist. Dichl. Pl. **2:** 392, 1832 = *Calliandra tetraphylla* (G. Don) Benth., Trans. Linn. Soc. **30:** 554, 1875.

I. tubulifera Benth. in Hook., Lond. Jour. Bot. **4:** 584, 1845 = *Pithecellobium tubuliferum* (Benth.) Pittier, Contr. U. S. Nat. Herb. **18:** 181, 1916.

Enumeration of the Species of Inga

Section I. Bourgonia Benth.

1. *marginata* Willd.
2. *longispica* Standl.
3. *fagifolia* (L.) Willd. ex Benth.
4. *coruscans* Willd.
5. *belicensis* Standl.
6. *pezizifera* Benth.

Section II. inga

Series 1. Punctatae J. León

7. *punctata* Willd.
8. *yunckeri* Standl.
9. *latipes* Pittier
10. *martinicensis* Presl
11. *brevipedicellata* Harms

12. *dominicensis* Benth.
13. *pinetorum* Pittier

Series 2. MULTIJUGAE J. León
14. *multijuga* Benth.
15. *thibaudiana* DC.
16. *skutchii* Standl.
17. *ruiziana* G. Don

Series 3. DENSIFLORAE J. León
18. *densiflora* Benth.
19. *schiedeana* Steud.
20. *micheliana* Harms
21. *squamigera* J. León
22. *davidsoniae* Standl.
23. *stenophylla* Standl.
24. *tenuipedunculata* J. León
25. *barbourii* Standl.
26. *hintoni* Sandwith
27. *calderoni* Standl.

Series 4. LEPTANTHAE Benth., emend.
28. *cookii* Pittier

Series 5. ACUMINATAE J. León
29. *acuminata* Benth.

Series 6. PILOSULAE J. León
30. *pilosula* (Rich.) Macbride
31. *hayesii* Benth.
32. *venusta* Standl.

Series 7. CALOCEPHALAE Benth.
33. *mucuna* Walp. & Duchass.
34. *venosa* Griseb. ex Benth.

Series 8. GOLDMANIANAE J. León
35. *goldmanii* Pittier

Series 9. DYSANTHAE Benth.
36. *standleyana* Pittier

Series 10. SPECTABILES J. León
37. *spectabilis* (Vahl) Willd.

Series 11. VULPINAE Benth.
38. *tonduzii* J. D. Smith

Series 12. TETRAGONAE Pittier
39. *sapindoides* Willd.

Series 13. INGA
40. *pauciflora* Walp. & Duchass.
41. *brenesii* Standl.
42. *oerstediana* Benth. ex Seem.
43. *edulis* Mart.
44. *latibracteata* Harms
45. *vera* Willd.
  45a. subsp. *vera.*
  45b. subsp. *eriocarpa* (Benth.) J. León
  45c. subsp. *spuria* (Willd.) J. León
46. *ingoides* (Rich.) Willd.
47. *coclensis* Pittier

Section III. LEPTINGA Benth.
48. *umbellifera* (Vahl) Steud.
49. *allenii* J. León
50. *portobellensis* Beurl.
51. *quaternata* Poeppig
52. *heterophylla* Willd.
53. *paterno* Harms
54. *mortoniana* J. León
55. *jinicuil* Schlecht.
56. *saffordiana* Pittier

INDEX OF LATIN NAMES

New taxa are in **boldface** type, all other taxa are in roman type; numbers in **boldface** type refer to descriptions, numbers in roman type refer to synonyms, numbers with dagger (†) refer to names incidentally mentioned.

Acacia 266†, 270†; berteriana 355†; pennatula 356†
Acaciae 266†
Affonsea 266†
Amosa 279
Calliandra 266†, 355†; canescens 355†; cumingii 356†; emarginata 355†, 356†; grandiflora 355†; houstoniana 355†; purpurea 356†; tergemina 356†; tetraphylla 356†
Cojoba 266†
Entada patens 356†
Enterolobium 266†; cyclocarpum 355†
Feuilleea 279; acuminata 313; coruscans 287; fagifolia 283; heterophylla 349; inga 336; ingoides 342; laurina 283; leptoloba 290; lindeniana 325; marginata 282; myriantha 345; oerstediana 330; panamensis 325; pezizifera 288; pilosula 315; punctata 290; quassiaefolia 315; quaternata 347; ruiziana 301; sapindoides 325; sciadon 345; setifera 315; spectabilis 322; spuria 339; stenocarpa 349; umbellifera 345; umbratica 345; xalapensis 339
Gliricidia sepium 273†
Hymenaea coubaril 356†
Inga 265-359†, **279;** sect. Bourgonia 267†, 269†, 275†, 276†, 280†, **281,** 290†; sect. Diadema 269†, 275†, 344; sect. Euinga 275†, 276†, 289, 311†, 322†, 330†; sect. Inga 265†, 267†, 276†, 280†, **289,** 290†, 354†; sect. Leptinga 269†, 275†, 276†, 277†, 281†, **344,** 353†, 354†; sect. Pseudinga 270†, 275†, 276†, 289; subsect. Grandiflorae 270†; subsect. Tenuiflorae 270†; ser. **Acuminata** 280†, **313;** ser. Calocephalae 267†, 276†, 280†, **317,** 318†; ser. **Densiflorae** 280†, **302,** 311†; ser. Dy-

santhae 267†, 380†, **320,** 322†; ser. **Goldmanianae** 280†, **319;** ser. Gymnopodae 276†; ser. Inga 268†, 269†, 281†, **328,** 330†, 344†; ser. Leptanthae 280†, **312;** ser. **Multijugae** 280†, **297;** ser. **Pilosulae** 276†, **314,** 354†; ser. **Punctatae** 276†, 280†, **289;** ser. **Spectabiles** 281†, **322;** ser. Sulcatae 322†, 328, 330†; ser. Tetragonae 269†, 276†, 281†, 311†, **324;** ser. Vulpinae 267†, 268†, 281†, 314†, **323;** acuminata 270†, 277†, 312†, **313,** 314†; adenophylla 368†, 320†; aestuarium 298, 299†, 301†; affinis 274†, 315; alatopetiola 325; **allenii** 265†, 344†, **346;** altissima 267†; angustifolia 314†; anomala 355†; antioquensis 325; barbata 274†; barbourii 302†, 303†, **308;** belicensis 276†, 281†, **287,** 288†; berteriana 339; billbergiana 355†; biolleyana 325, 328†; boliviana 348†; brenesii 328†, **330;** brevipedicellata 290†, **295,** 296†; brunnescens 299†; caldasiana 287; calderoni 303†, **311;** camuriensis 325; canescens 355†, caracasana 325; chardonii 325; chartana 330; chiriquensis 330; ciliata 313†; cinnamomea 274†, 277†; cobanensis 330, 332†; coclensis 328†, 329†, **343,** 344†; cognata 355†; confusa 301; conglomerata 348†; cookii 267†, **312,** 313†; cordistipula 277†; 347†; coriacea 346†, 355†; coruscans 276†, 281†, 283†, **287†,** 295†; culagana 330; cyclocarpa 355†; cylindrica 283†; davidsoniae 302†, 303†, 304†, **307;** densiflora 268†, 270†, 274†, 302†, **303,** 304†, 305†, 306†, 307†; dominicensis 273†, 290†, **296,** 297†; donnell-smithii 339, 343†; dysantha 322†; edulis 268†, 274†, 275†, 278†, 328†, 329†, 332†, **333,** 334†, 343†, var. grenadensis 330, 332†, var. minutiflora 330, 332†, var. typica 333†; eggersii 325; elegans 355†, emarginata 355†; endlicherii 333†; endlichii 334; englessingii 355†; eriocarpa 338, 342†; eriocarpoides 342†; eriorhachis 330, 332†, 344†; excelsa 282; fagifolia 273†, 275†, 276†, 277†, 281†, **283,** 284†, 286†, 288†, 301, 350†; fasciculata 333†; fastuosa 276†, 317†, 318†, 319†; feuillei 268†, 271†, 274†; fissicalyx 339, 342†; flexuosa 304; foetida 355†; foliosa 301; fragrans 355†; fulgens 322; galibica 342; gigantifoliola 355; gladiata 299; globulifera 355†; goldmanii 268†, **319,** 321†; gracilipes 345; grandifolia 325; guadalupensis 355†; guatemalensis 355†; guayaquilensis 282; hartii 325; hayesii 268†, 277†, 314†, **316,** 317†; heinei 304†; heterophylla 269†, 345†, **349,** 350†; hintoni 302†, 303†, **310;** hirsutissima 323†; houstonia 355†; ierensis 290; inflata 277†; 347†; inga 336; ingoides 329†, **342,** 343; java 304†; jimeneziana 325; jinicuil 270†, 274†, 277†, 296†, 345†, 351†, **353;** laevigata 355†; lamprophylla 336; langlassei 303, 304†; lateriflora 349†; latibracteata 329†, **334;** latipes 290†; 293†; **294;** latifolia 356†; laurina 283, 286†, 350†; lawrenceana 345; leptantha 313†; leptoloba 292†; 293†; leucantha 356†; limonensis 304†; lindeniana 325†; longispica 276†, 281†, **283;** lopadenia 287†; lucida 322; macradenia 299; macrocarpa 356†; macrophylla 276†, 317†, 319†, 346; mapiriensis 349; marginata 268†, 272†, **281,** 283†; martinicensis 273†, **294,** 295, 296†, 297†; mathewsiana 349†; maxoniana 347; membranacea 356†; merianae 342; micheliana 302†, 303†, 304†, **305,** 332†; microdontha 304†; microstachya 288; mociniana 339; mollifoliola 303; montealegrei 303, 304†; monticola 303; **mortoniana** 265†, 268†, 277†, 345†, 346†, **351,** 352†; mucuna 276†, **317,** 318†, 319†; multijuga 270†, **298,** 299†, 300†, 301†; mutisii 347; myriantha 345; nitida 315; nitens 355†; nobilis 349†; odorata 282; oerstediana 267†, 274†, 278†, 328†, 329†, **330,** 332†, 333†, 334†; oophylla 338, 339†; pamplonae 330; panamensis 325, var. clavata 325, 328†, var. pittieri 325, var. rodrigueziana 325; panuriensis 349†; pardoana 349†; patens 356†; paterno 274†, 277†, 345†, **350,** 351†, 353†; pauciflora 328†, **329,** 330†; peckii 356†; pennatula 356†; pezizifera 276†, 281†, **288;** pilosiuscula 315; pilosula 268†, 270†, **314,** 315†; pinetorum 280†, 290†, **297;** pittieri 325; platycarpa 315; papayanensis 290; portobellensis 277†, 344†, **346;** preussi 325; pringlei 304; protracta 349; pruriens 268†, 320†; psitacorum 313†; puberula 282; punctata 268†, 272†, 274†, 277†, 289†, **290,** 292†, 293†, 294†, 296†, 297†, subsp. chagrensis 290, var. panamensis 290; pungens 356†; purpurea 356†; purpusii 325; pychnostachyla 282; quassiaefolia 314; quaternata 269†, 272†, 345†, **347,** 348†, 349†; radians 350, 351†; recordii 299; rensoni 325; rodrigueziana 325; roussoviana 347; rubiginosa 322†, 344†; rufescens 356†; ruiziana 268†, 275†, 280†, 288†, 298†; 299†, **301;** saffordiana 268†, 270†, 277†, **354;** salvadorensis 325; saman 356†; santanderensis 347; sapida 281; sapindoides 268†, 274†, 276†, **325,** 327†, 328†; schiediana 302†, 303†, **304,** 305†; schippii 347; sciadon 345; sciadodendron 334; semialata 282; semicordata 356†; sericea 355†; sessilis 319†, 320†; setifera 315; skutchii 280†, 298†, **300;** smithii 322, 323†; sordida 303, 304†; speciosa 355†, 356†; speciosissima 274†; spectabilis

274†, **322,** 323†; spuria 339, 342†; **squamigera** 265†, 303†, **306;** standleyana **321,** 322†; stenophylla 302†, 303†, **307,** 308†; stevensoni 356†; strigillosa 293†; subsericantha 289†; subvestita 312; tarapotensis 349†; tenuiflora 299; **tenuipedunculata** 265†, 303†, **308;** tergemina 356†; tetraphylla 283, 356†; thibaudiana 272†, 277†, 298†, **299,** 300†; tiribiana 304†; tonduzii 323†, **324,** 325†; tubulifera 356†; tuerckheimii 330; umbellata 349; umbellifera 344†, **345,** 346†; umbratica 345; urabensis 314†; uraguensis 274†, 275†, 342†; venosa 273†, 276†, 317†, **318,** 319†; venusta 277†, 314†, **316,** 317†; vera 272†, 277†, 278†, 279†, 328†, 329†, 333, **335,** 342†, 343†, subsp. **eriocarpa** 336†, **338,** subsp. lamprophylla 336, subsp. portoricensis 336, subsp. **spuria** 335†, 336†, **339,** subsp. vera **336,** 337†, 339†, var. lamprophylla 336, var. portoricensis 336; vulpina 323†; williamsii 347; wittiana 348†; xalapensis 339; ynga 333; yunckeri 290†, **293;** zapacuanica 334, 335†
Ingae 266†
Ingaria 279
Leguminosae 265†, 267†, 272†, 320†
Lysiloma 266†
Mimosa 266†, 270†; coriacea 295†; coruscans 287; fagifolia 283, 286†, 294; guatemalensis 355†; inga 335, 337†; ingoides 342, laurina 283; lucida 315; nitida 315; parae 349; pilosula 314, quassiaefolia 315; semialata 281; sericea 290, 294, 295†; spectabilis 322; spuria 339; tetraphylla 283; umbellifera 345; ynga 333
Mimosaceae 265†, 267†, 269†
Mimosae 266†
Piptadenia foetida 355†
Pithecellobium 266†, 268†, 272†, 355†; sect. Caulanthon 266†; belizense 356†; cognatum 355†; dulce 356†; englesingii 355† **gigantifoliolum** 355; latifolium 356; tum 355†; dulce 356†; englesingii 355†; saman 356†; stevensoni 356†; tubuliferum 356†; unguis-cati 355†
Swartzieae 269†
Torealia 279
Zygia 266†

DUKEA, A NEW GENUS OF THE RUBIACEAE (TRIBE MUSSAENDEAE)

BY JOHN D. DWYER
St. Louis University and Missouri Botanical Garden, St. Louis.

ABSTRACT

The arborescent or shrubby genus *Dukea* of the tribe *Mussaendeae* (*Rubiaceae*) is described as new. The five new species are from five provinces of Panama with the majority at elevations from 2,000 to 3,000 feet. One species from Colombia, *D. chariantha* (Standley) Dwyer is a new combination. The structure of the multiovulate ovary with its septum disposed medianally or, in one species, as a parietal ridge, is an important generic character.

Several years ago I found in the herbarium of the Missouri Botanical Garden a Pittier collection (*4223*) of a woody rubiaceous plant in flower, collected on August 1911 at Dos Bocas, Río Fatô Valley, Province of Colon, Panama. Pittier had simply written *Coussarea* on the label and appended no descriptive field data concerning the plant. Floral dissection reveals that the ovules are numerous and arise from the median septum of the 2-celled ovary. This immediately rules out the possibility of its being a *Coussarea* and reduces its tribal position in the *Rubiaceae* to the first seven tribes according to the arrangement adopted by Standley from Wernham (Jour. Bot. **54:** 322-334, 1916) for the New World genera. The presence of valvate corolla lobes immediately eliminates two of these seven tribes and the fact that the collection lacks spines does not suggest the *Naucleeae.* The *Hedyotideae* made up mostly of herbaceous plants with laciniate stipules may be readily set aside. Inasmuch as the Pittier collection lacks fruit, an impasse may be reached in choosing between the three remaining tribes, *Mussaendeae, Cinchoneae,* and *Condamineae,* although general floral structure scarcely suggests the *Cinchoneae.*

Obviously vegetatively and florally similar, but not conspecific with the Pittier material, is a collection of a small tree, 6-10 ft high and bearing white flowers, made in 1940 by Terry & Terry (*1847*) at the Cana-Cuasi Trail (Camp 2) in the Chepigana District of the Province of Darien, Panama. Its general vegetative habit including the entire stipules, in addition to its 2-celled ovary with numerous ovules arising from a median septum and its valvate corolla lobes, leaves no doubt of its kinship with the Pittier collection. Standley named this *Coussarea colonis* but the binomial is a nomen rejiciendum.

On January 26 of this year Dr. Edwin Tyson, Mr. Kurt Blum and myself collected on Cerro Jefe, Province of Panama, in a mist-swept *Clusia* forest at 2700-3000 ft, a solitary collection of a small tree in mature fruit. Its foliage and stipules bear a striking resemblance to the aforementioned species. Fortunately one flower was available for dissection and this left no doubt as to the relationship of the three collections. Its baccate fruit immediately eliminates the tribe *Cinchoneae* and *Condamineae* and leaves only the tribe *Mussaendeae.* The fruit, in fact, supplied the key to several flowering rubiaceous collections which seem to defy classification or were erroneously placed in *Coussarea.*

ANN. MISSOURI BOT. GARD. **53** (3): 360-367, 1966.

The tribe *Mussaendeae*, if we are to follow Standley's numerous treatments of the *Rubiaceae* on a national basis, e.g. Colombia (Publ. Field Mus. Nat. Hist., Bot. Ser., **7:** 1-176, 1930); Ecuador (loc. cit. 177-252); Bolivia (loc. cit. 341-486); Costa Rica (loc. cit. **18:** 1264-1380, 1938), has only two genera with terminal inflorescences, *Gonzalagunia* and *Isertia*. Unlike the two collections under study, *Gonzalagunia* has elongate spiciform inflorescences while *Isertia* has an ovary with four to six cells and a much more coarse inflorescence. Interestingly enough the foveolate seeds of our collection serve to strengthen the proposed kinship with *Gonzalagunia* and *Isertia* (as well as suggesting possible affinities with certain genera of the *Gardenieae*, e.g. *Hamelia, Hoffmannia, Bertiera*, well known in the tropics of the New World). Bremekamp (Verh. Kon. Nederl. Akad. Wet., Afd. Natuurk., Sect. 2, **48:** 1-297, 1952), Verdcourt (Bull. Jard. Bot. État Brux. **28:** 209-290, 1958), and Petit (Bull. Jard. Bot. État Brux. **34:** 1-229, 1964) have stressed the importance of seed anatomy in the *Rubiaceae*.

The site of our collection, Cerro Jefe, is on the Atlantic slope of the Continental Divide, a fact which fits in well with the site of Pittier's collection from the Province of Colon. The summit of Cerro Jefe, presumably visited previously by only one plant collector, Paul Allen, is currently under study by the author as it promises to yield a modicum of new species of phanerogams, principally in the *Rubiaceae*.

A study of these three Panamanian collections suggests the establishment of a new genus. A collection by Lawrance (*575*) in 1932 from El Humbo, State of Boyaca, 130 miles north of Bogota, Colombia, at approximately 2300 ft elevation was described by Standley as *Coussarea chariantha*. It is a low shrub with white flowers. The multiovulate and biloculate ovary coupled with other floral and vegetative characters readily links it with the Panamanian collections under consideration.

A collection made by Duke (*6099*) on Cerro Pirre, Province of Darien, Panama, obviously belongs to the new genus. Cerro Pirre, a rich but little known collecting area in Panama (Dwyer, Ann. Missouri Bot. Gard. **51:** 110, 1964) is located more on the Pacific side of the Republic. It is appropriate to remark that the new genus, while admittedly known only from a handful of collections, seems to favor altitudes above 2,000 ft and to hug the Continental Divide on the Costa Rica-Panama border into central Panama, swinging in hook-like style toward the Pacific side at the Colombia-Panama border.

The last species to be included in the new genus is described from two collections from the Province of Bocas del Toro, Panama, one by Cooper (*228*) and a collection by von Wedel (*2248*), labelled in the Missouri Botanical Garden herbarium by Standley as *Coussarea colonis* Standley. Both are low trees with white flowers. Only in the structure of the placentae and the presumed abortion of the ovarian septum do the two collections show a radical departure from the other material placed in the new genus.

In five species of the new genus the ovarian septum is clearly seen in transverse section as a median partition with the ovules disposed in four clusters, two per locule. The placentation is thus axile. On the other hand, a cross-section of

the ovary of *von Wedel 2248* and *Cooper 228* made above the base, usually reveals four clusters of ovules, each pair of clumps flaring out from a thickened placenta which extends up the ovarian wall and intrudes itself into the locule, but is not sufficiently intruded as to join the placenta opposite and thus fashion a median septum. The ovary is thus uniloculate and the placentation is parietal. The ovary of this species, as well as those of the other species of the new genus, demands careful dissection. The failure to dissect critically the ovary of some species labelled *Coussarea* has caused much difficulty.

DUKEA Dwyer, gen. nov. (tribe *Mussaendeae*)

Arbores parvae vel frutices, ramulis teretibus. *Folia* brevipetiolata lanceolata acuminata papyracea vel crasso-papyracea, venis lateralibus late arcuatis evidenter distantibus infra prominulis; stipulae lineari-subulatae ad triangulares conspicuae plerumque persistates. *Inflorescentiae* terminales corymboso-paniculatae, bracteis subulatis subpersistentibus, bracteolis ad basin pedicellorum affixis. *Flores* multi pedicellati, hypanthio parvo, calyce minore coronario, dentibus 4-5 minutis; petala alba, tubo cylindrico angusto, in gemmis contorto, lobis quam tubo brevioribus, angustis, valvatis reflexisque post anthesin contortis; antherae 4-5 lineari-lanceolatae, filamentis brevibus ad basin tubi affixis; ovarium biloculatum, septo medio, placentis mediis axillaribus, in uterumque loculum bifurcate extantibus, ramis placentarum ultime membranaceis, vel ovarium uniloculatum, utraque placenta parietale prime a basi ovarii oriente tunc bifurcata. *Fructus* parvi cocco-baccati, seminibus multis rotundis foveolatis.

Type species: *Dukea panamensis* Dwyer.

The new genus is named in honor of Dr. James Duke, distinguished ecologist and student of the flora of Panama.

a. Ovary biloculate; inflorescences 15-30 cm long (Section *Dukea*).
  b. Inflorescence patulous, 15-30 cm wide; leaves glabrescent above.
    c. Leaves oblong-lanceolate, scarcely falcate, the blade 2-3 times longer than wide.
      d. Petioles up to 2 cm long; corolla tube glabrous to glabrescent without; anthers ca 2.5 mm long, acute to subobtuse at the apex; Colombia .... 1. *D. chariantha*
      dd. Petioles up to 6 cm long; corolla tube obviously pubescent without; anthers up to 4 mm long, attenuate at the apex; Panama ...... 2. *D. panamensis*
    cc. Leaves narrowly lanceolate, obviously falcate, the blade more than 3 times longer than wide .... 3. *D. victoriae*
  bb. Inflorescence contracted, not more than 6 cm wide; leaves appressed-pilose above.
      d. Leaves up to 13.5 cm wide; petioles up to 4 cm long; flowers ca 1.5 cm long; lower half of peduncle unbranched .... 4. *D. blumii*
      dd. Leaves up to 8 cm wide; petioles ca 1 cm long; flowers ca 1 cm long; lower half of peduncle branched .... 5. *D. darienensis*
aa. Ovary uniloculate; inflorescences up to 6.5 cm long (Section *Uniloculata*) .... 6. *D. euryphylla*.

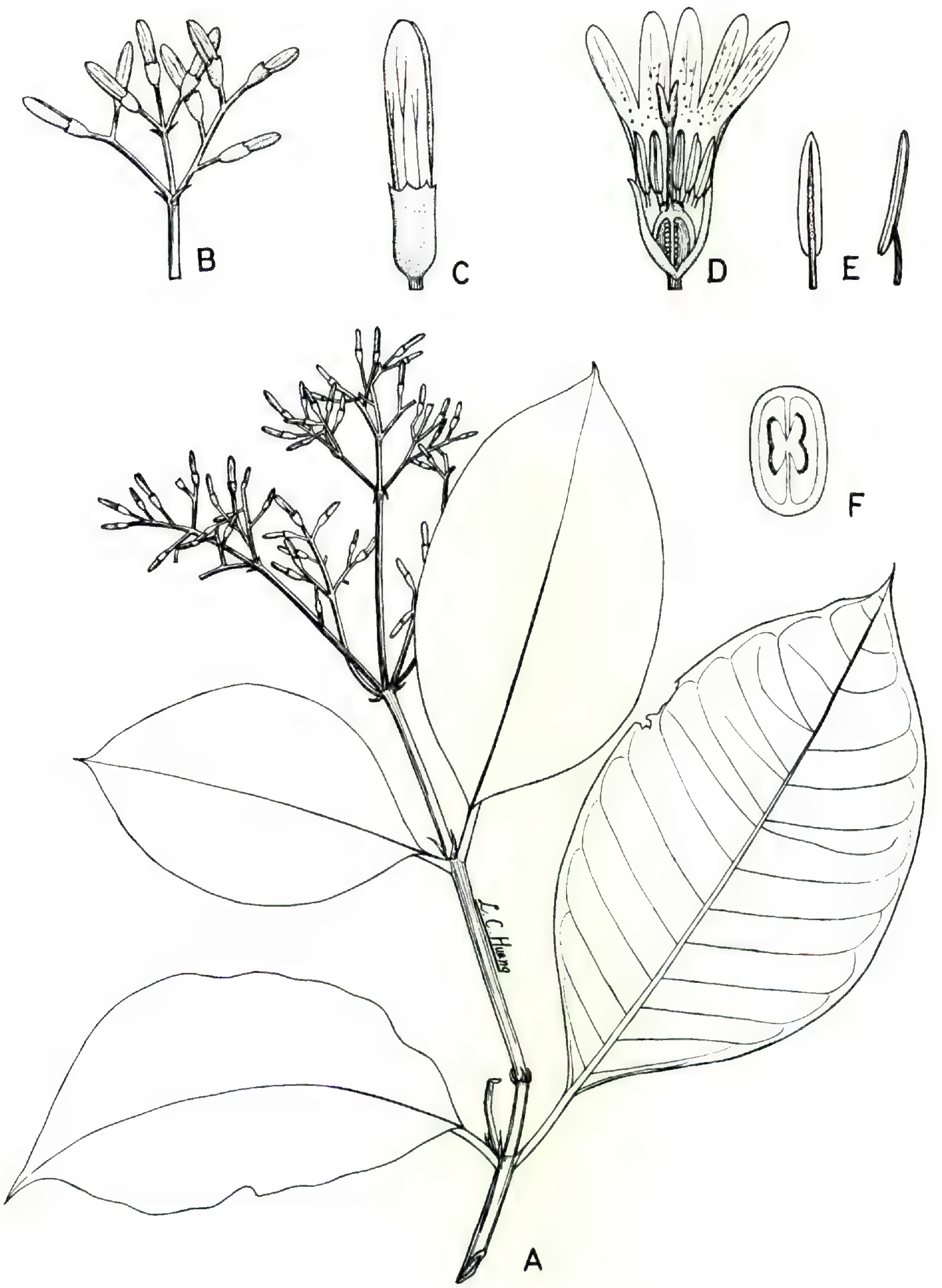


Fig. 1. *Dukea chariantha* (Standley) Dwyer. A, habit (× ⅔); B, cymule (× 2); C, bud (× 7); D, flower (× 10); E, anthers (× 17); F, cross-section of ovary, much enlarged. After *Lawrance* 575 (MO).

1. Dukea **charintha** (Standley) Dwyer, comb. nov.—Fig. 1 (A-F).

Coussarea chariantha Standley, Publ. Field Mus. Nat. Hist., Bot. Ser., **11:** 195, 1936.
Colombia. boyaca: El Humbo, *Lawrance 575* (MO, F, type of *Coussarea chariantha*).

2. Dukea **panamensis** Dwyer, sp. nov.

Arbores parae, ad 3 m altae, ramulis glabrescentibus. *Folia* petiolata, petiolis 2-5.5 cm longis, ad 0.35 cm latis, stipulis triangularibus, ad 1.5 cm longis, ad 0.6 cm latis, arachnoideo-pubescentibus; lamina elliptico-lanceolata (folia maioria), 17-35 cm longa, 6-13.5 cm lata, apice brevi-acuminata et ultime acutissima, basi attenuato-acuta, crasso-papyracea, venis lateralibus 12-17, eis mediis 1.5-2 cm distantibus. *Inflorescentiae* patulae, ad 23 cm longae, ad 28 cm latae, pyramidatae, pedunculo ad 3 mm lato, pubescente, ramis basalibus forte divergentibus, ad 12 cm longis, ramis superioribus paucis distantibus, cymulis (hic in fructu visis) conspicue patulis pauci-floriferis. *Flores* ca 13 mm longi, pedicellis ad 0.7 cm longis, plano-compressis desuper pubescentibus, bracteolis subulatis, ad 3 mm longis, deciduis; hypanthium rotundum, ca 1.5 mm longum, sparse pubescens, calyce coronario truncato, ad 1 mm longo, dentibus 4, minutis; corolla ca 10.5 mm longa, tubo cylindrico, ca 1 mm lato, intra farinoso, extus pubescente, lobis 4 linearibus, ad 6 mm longis, intus farinosis; antherae 4 lineari-subulatae, ad 4.5 mm longae, attenuato-acuminatae; ovarium septo medio angusto. *Fructus* pedicellati, pedicellis filiformibus, ad 10 mm longis, coccis rotundis, ad 0.5 cm longis, in sicco nigris sparse puberulis, venis paucis gracilibus longitudinalibus, seminibus rotundis, ca 0.4 mm longis, conspicue foveolatis luteis.

Panama. panama: Cerro Jefe, 2600-3000 ft elev, *Tyson, Dwyer & Blum 3326* (holotype MO).

3. Dukea **victoriae** Dwyer, sp. nov.

Frutices ramulis pubescentibus. *Folia* petiolata, petiolis ad 3 cm longis, ca 1.3 mm latis, stipulis triangularibus, ad 1.5 cm longis, acutissimis pubescentibus; lamina falcato-lanceolata, 16-27 cm longa, 3.5-8 cm lata, apice attenuato-falcato-acuminata papyracea, supra glabrescens infra auro-villosula praecipue in venis, venis lateralibus ad 20, eis mediis 1.5-2 cm distantibus. *Inflorescentiae* certe ad 8 cm latae, patulae, pedunculo ad 5.5 cm longo, ad 0.2 cm lato, pubescente, ramis divergentibus, hic ad 3.5 cm longis, cymulis subflabellate dispositis. *Flores* pedicellis ad 6 mm longis, gracilibus pubescentibus, bracteis subulatis, ad 3 mm longis, bracteolis minutis; hypanthium urceolatum, ad 2 mm longum, sparse pubescens, calyce coronario, ad 1 mm longo, truncato, dentibus 4, minimis; corolla tubo cylindrico, hic ad 2.5 mm longo, 0.8 mm lato, omnino glabro, lobis quam tubo paulo longioribus subcarnosis; antherae 5 lineares, ca 2 mm longis, apice attenuatae sed obtusae, filamentis ad 0.8 mm longis, ad basin tubi affixis; ovarium biloculatum, septo medio, stylo ad 1 mm longo, stigmatibus linearibus, ad 1 mm longis, rectis. *Fructus* non visi.

Panama. darien: cloud forest, Cerro Pirre, *Duke 6099* (holotype MO).

The new species is named in honor of Sister M. Victoria Hayden who assisted the author in several floral dissections of the new genus and numerous dissections of *Coussarea*. The inflorescence of the type is somewhat fragmentary and the floral dissection was made from a late bud stage.

4. DUKEA **BLUMII** Dwyer, sp. nov.

Arbores ?, ramulispubescentibus. *Folia* petiolis 1-4 cm longis, ad 0.3 cm latis, stipulis triangularibus, ad 1 cm longis, arachnoideo-pubescentibus; lamina lanceolata vel ovata-lanceolata, 25-38 cm longa, 9-13.5 cm lata, apice brevi-acuminata et triangulari-acuta, basi acuta, papyracea, venis lateralibus 16-20, eis mediis 1.5-2.5 cm distantibus. *Inflorescentiae* subcylindriformes ad 15 cm longae et 5 cm latae, pedunculo plano-compresso villosulo ad 10 cm longo et 0.25 cm lato, ramis paucis geminatis basi dilatatis fortiter ascendentibus, ad 1.5 cm longis, cymulis patulis pauci-floriferis. *Flores* ad 13 mm longi, pedicellis ad 0.5 cm longis, dense auro-pubescentibus, bracteolis ca 0.5 mm longis, deciduis; hypanthium subfusiforme-urceolatum, ad 3 mm longum, puberulum, calyce brevi, dentibus 5 minutis, ca 0.3 mm longis; corolla ad 9.5 mm longa, tubo angusto-cylindrico (in gemmis vix falcate disposito) extus pubescente, lobis 4 lineatibus, ad 6 mm longis; antherae lineari-subulatae, ad 4 mm longae, attenuato-acuminatae, filamentis ad 2 mm longis; ovarium biloculatum, septo medio angusto, stylo lobis linearibus rectis, ca 2 mm longis. *Fructus* non visi.

PANAMA. COLON: vic Dos Bocas, Río Fatô Valley, *Pittier 4223* (holotype MO).

5. DUKEA **DARIENENSIS** Dwyer, sp. nov.

Frutices vel arbores parvae, ad 3 m altae, ramulis diffuso-pilosis. *Folia* petiolis ad 1 cm longis, ca 1 cm latis, stipulis triangularibus, ad 0.7 cm longis, pubescentibus; lamina lanceolata, 15-25 cm longa, 6-8 cm lata, acumine ad 1 cm longo, basi ob-triangularis papyracea, venis lateralibus 12-16, eis mediis 1-1.5 cm distantibus. *Inflorescentiae* ad 11 cm longae, ad 6 cm latae, pedunculo villoso, ad 3 cm longis, ramulis gracilibus, ad 2.5 cm longis, bene distantibus, corymbis terminalibus patulis, floribus in uteroque primo ramulo ca 7-5, bracteis bracteolisque subulatis parvis. *Flores* ad 11 mm longi, pedicellis ad 0.25 cm longis, auro-puberulis; hypanthium urceolatum, ca 1 mm longum, villosulum, calyce brevi coronario, ad 1.3 mm longo, dentibus 5 evanescentibus; corolla 4-5 mm longa, tubo in gemmis deorsum angustiore tunc cylindrico, ca 0.8 mm lato, extus puberulo, lobis 4 (-5?) linearibus, ad 4 mm longis; antherae 5 lineares, ca 3 mm longae, filamentis ca 1 mm longis; ovarium septo medio gracili, stylo lobis terminalibus, ca 2.5 mm longis, rectis. *Fructus* non visi.

PANAMA. DARIEN: Cana-Cuasi Trail (Camp 2), Chepigana district, *Terry & Terry 1487* (holotype MO).

Standley was suspicious of the wisdom of his decision to include the collection cited above in his *Coussarea colonis* Standley (Field Mus. Nat. His., Bot. Ser., **22**: 180, 1940); he remarks ". . . [it] differs from the type (of *C. colonis*) in having

leaf blades only 4.5-5.5 cm wide and smaller flowers, with the corolla tube but 5 mm long." The problem associated with Standley's concept of *Coussarea colonis* is discussed below.

Sectio **UNILOCULATA** Dwyer, sect. nov. Ovarium uniloculatum; inflorescentiae breves. Type species *Dukea euryphylla* (Standley) Dwyer.

6. DUKEA **EURYPHYLLA** (Standley) Dwyer, comb. nov.

Coussarea euryphylla Standley, Publ. Field Mus. Nat. Hist., Bot. Ser., **4:** 294, 1929.
C. colonis Standley, loc. cit. **22:** 179, 1940, nomen rejiciendum.

Trees up to 4.5 m tall; branchlets glabrous. Leaves with petioles 2-3 cm long, up to 0.3 cm wide; stipules triangular, up to 1.2 cm long, presumably glabrous; blade lanceolate or somewhat falcate-lanceolate, 27-35 cm long, 10-12 cm wide, the acumen up to 1 cm long, thickly papyraceous, the lateral veins 17-20, the median ones 1-2 cm apart. *Inflorescence* patulous, up to 8 cm long and 6 cm wide, the peduncle ca 2 cm long, slender, ca 1 mm wide, the branches few, up to 2 cm long, the cymules few-flowered. *Flowers* 12-15 mm long; pedicels up to 0.35 cm long, puberulent; bracts subulate, up to 2 mm long; bracteoles minute; hypanthium urceolate, 2-3.5 mm long, moderately puberulent, the calyx 1-1.5 mm long, crown-like, the teeth 5, minute; corolla 9-15 mm long, the tube cylindrical, puberulent; anthers 5, linear-subulate, up to 4 mm long, attenuate-acuminate; ovary uniloculate, the placentae 2, parietal and arising from the base of the locule, soon bifurcating, the style lobes 2, terminal, subulate, ca 2 mm long. *Fruit* not seen.

PANAMA. BOCAS DEL TORO: Fish Creek Mts, vic Chiriqui Lagoon, *von Wedel 2248* (MO); Almirante (or Buena Vista Camp on Chiriqui Trail?), *Cooper 228* (F, type of *C. euryphylla*).

As the synonomy cited above indicates, Standley described *Coussarea euryphylla* in 1929 from a collection by Cooper (*228*) which he indicated came from the Buena Vista Camp on the Chiriqui Trail, Bocas del Toro, Panama. In 1940, in describing *C. colonis* from Bocas del Toro, Standley designated *Cooper 228* as the type indicating Almirante as the collection site. On examining the types of both species in the Chicago Natural History Museum I found that they appear to be based on the same collection, the disparity in collection sites notwithstanding.

Unfortunately, too, Standley failed to observe the uniloculate nature of the ovary of his bilocated type, as well as the fact that the placentae arise basally and extend up the wall with each intruding itself and bifurcating, and the numerous ovules disposed as clusters on the membranaceous placental branches.

The author wishes to thank Mrs. L. C. Huang who prepared the plate for this paper.

Addendum

Dr. James Duke in 1962 collected (*5337*) what is presumably a woody rubiaceous shrub with white flowers on Cerro Pirre in the Province of Darien, Panama. Superficially its fruiting inflorescence appears like a *Bertiera* of the *Gardenieae* but

the pedicellate, rotund, baccate fruit with foveolate orange seeds strongly resembles the fruit of *Dukea panamensis;* in addition the general character of the foliage immediately suggests the genus *Dukea.* The marcescent surface of many of its fruits is noteworthy but it is probably an artifact created in drying. In the absence of flowers and considering that the specimen vegetatively is in poor condition, I have hesitated to describe it as a new species.

NOTES ON COUSSAREA (RUBIACEAE), ESPECIALLY THE PANAMANIAN SPECIES

BY JOHN D. DWYER
St. Louis University & Missouri Botanical Garden
and SISTER M. VICTORIA HAYDEN, St. Louis University[1]

ABSTRACT

The history of the New World tribe *Coussareae* (*Coussarea* Aubl. and *Faramea*) is discussed in detail. Included is a table of diagnostic characters separating the tribes *Coussareae* and *Psychotrieae*. Eight species of *Coussarea* found in Panama are presented together with a key to species including the newly described *C. cerroazulensis* Dwyer.

The tribe *Coussareae* was established in the *Rubiaceae* by J. D. Hooker in 1873 (Gen. Pl. **2:** 7-151) when he included it with the *Psychotrieae* in his tribal series C made up of 13 tribes. In segregating the *Coussareae* and *Psychotrieae*, Hooker distinguished these and six other tribes by the presence of an inferior radicle in contrast to the five others having a superior radicle. He set apart the *Coussareae* from the *Psychotrieae* on the basis of the former possessing an evanescent septum and a 1-seeded fruit, and included in the tribe three tropical American genera: *Faramea*, *Coussarea*, and *Homoclados*. Mueller in 1881-1885 (in Mart., Fl. Bras. **6** (5): 78-162) reduced *Homoclados* to a section of *Faramea* and employed the position of the ovules and that of the seed as generic characters: *Faramea* with the seed placed horizontally; *Coussarea* with a single, erect seed. Mueller's distinction set the pattern for subsequent treatments of the New World members of the *Coussareae* by Schumann (Pflanzenfam. **4:** 96-156, 1891), Wernham (Jour. Bot. **54:** 322-334, 1916), Standley (Publ. Field Mus. Nat. Hist., Bot. Ser., **7:** 1-353, 1931), Bremekamp (Rec. Trav. Bot. Neerl. **31:** 248-308, 1934), Verdcourt (Bull. Jard. Bot. État Brux. **28:** 209-290, 1958) and many others.

Although the tribe *Coussareae* is related to the *Psychotrieae* as one of ten tribes described as having a single ovule per locule, further characters must support its position there because the *Coussareae* often have two ovules in a single locule. Baillon (Hist. Pl. **2:** 256-503, 1881) emphasized the fact that the two ovules, when present, really belong to two cells, though they may, and usually do contact each other. Wernham (loc. cit.) inserted a parenthetical statement in his key to the effect that this contacting of ovules results from the evanescent character of the septum in the *Coussareae*. Standley in various treatments of the *Rubiaceae* in the New World on a national basis from 1930 to 1949, while not discussing this important point, did utilize the character, "ovary 1-celled, or 2-celled, but with a very thin septum," in separating the *Coussareae* from the *Psychotrieae*. The very thin septum has traditionally separated the two tribes from the time of de Candolle (Prodr. **4:** 341-621, 1830). Similarity of growth habit and leaf form, valvate

[1] Parts of this paper were submitted by the junior author in partial fulfillment of the degree of Master of Science at St. Louis University.

ANN. MISSOURI BOT. GARD. **53** (3): 368-374, 1966.

Table 1. Comparison of the tribal characteristics of *Psychotrieae* and *Coussareae*

Character	PSYCHOTRIEAE	COUSSAREAE
Habit	Trees or shrubs, rarely creeping herbs (*Geophila*)	Trees or shrubs, no genus herbaceous
Leaves	Usually membranous, growing at acute angle toward apex of branch (*Rudgea* excepted)	Often coriaceous, growing at right angle to branch
Stipules	Usually bifid, lobes variable; sometimes entire (*Psychotria*); when connate, then bifid	Usually entire from an ovate-triangular base; sometimes awned (*Faramea*) when connate, then entire
Bracts	Often present (*Geophila* and *Cephaelis*, large, colored, involucrate), usually small	Present or absent, usually very small (*Faramea*, few species, two large bracts at base of inflorescence)
Inflorescence	Terminal or axillary, often many flowered, lax, or dense capitula, thyrsoid panicles	Terminal, rarely axillary, often loose, decussate panicles or umbellate cymes, ultimately cymes
Flowers	5-merous (except in *Declieuxia* and *Pagamea*); sessile or pedicellate	4-merous, very rarely 5-merous; stout pedicels, rarely sessile flowers
Calyx lobes	tube usually ± pubescent; valvate lobed; cupular receptacle, persistent in fruit	same
Corolla	Tubular, short rarely elongate, or hypocrateriform; lobes variable, many horned; interior tube usually ± pubescent; valvate in bud	Tubular; usually elongate; throat rarely expanded; lobes thickened, usually reflexed; interior tube glabrous; valvate in bud
Stamens	Filamentous, attached in throat; anthers oblong, dehiscing longitudinally	same
Style	Bifid with length variable, included or exserted, lobes usually linear	same
Ovary	Bi-locular, 2 erect ovules; septum thick	Bi-locular, 2 erect ovules; septum evanescent or incomplete; ovules connate
Fruit	Oval or globose drupe; soft, hard or leathery exocarp; endosperm horny, variously grooved or smooth; 2-seeded	Leathery oval drupe; endosperm horny; 1-seeded by fusion of ovules or by abortion of one ovule; longer than broad or depressed (*Faramea*)

aestivation, elongate and longitudinally dehiscent anthers, as well as fleshy fruits support this relationship. Verdcourt (loc. cit.) says that the comparative character of aluminum accumulation confirms the association of the tribes *Psychotrieae, Coussareae,* and *Morindeae.* Metcalf & Chalk (*Anatomy of the Dicotyledoneae* **2:** 759-776, 1950) reported raphides in the three tribes, and Bremenkamp (cf. Verdcourt, loc. cit.) suggested these as possibly being valuable distinguishing characters. The pollen of *Coussarea* appears to be unique among the *Rubiaceae,* being cylindrical rather than spherical (Erdtman, *Pollen Morphology and Plant Taxonomy* 383-387, 1952). Verdcourt (loc. cit.) and Baker (Evolution **10:** 23-31, 1956) reported the pollen of *Faramea* as triporate and tetraporate with bulbous aperture membranes. Erdtman (loc. cit.) studied about 20 species and found that this condition is characteristic of the genus.

The pistil of *Coussarea* has an extremely small ovary in which the septum is usually paper-thin with the two ovules connate, and often scarcely distinguishable from the ovarian wall. The septum, though very thin in comparison with the relatively thick septum of *Psychotria,* is complete in *Coussarea.* The erect ovules are longer than broad. Contrastingly, in *Faramea,* the ovules are about as long as broad and are almost circular; they tend to coalesce near the center of the locule or else to be so closely associated laterally that they are difficult to separate on dissection. In *Coussarea* a longitudinal section of the ovary shows a triangular septum whereas in *Faramea* such a section fails to show any clearcut septum. The ovary of *Faramea,* when sectioned transversely near the apex, shows a single locule; if the section is basal, the 2-loculate condition is occasionally apparent. The best section is a longitudinal one, made with care in order not to dislodge the ovules from the septum or from each other.

The ovule and fruit characters are the deciding factors in the separation of the tribes *Coussareae* and *Psychotrieae.* Table 1 lists other characters which correlate well with carpellary features but which in themselves do not represent strong distinguishing characters. The 4-merous condition of the flower is relatively constant in the *Coussareae* but admittedly is found in several genera of the *Psychotrieae.* A lack of pubescence within the corolla and thickened corolla lobes generally characterize *Coussarea* and to some extent *Faramea* and these may prove helpful in determining the tribe. The characteristic single-aristate or triangular stipules and the typically lax inflorescences are often good indications that a species is a member of the *Coussareae.*

As a consequence of the abortion of one ovule, *Coussarea* fruits are one-seeded (Schumann, loc. cit.) The vestige of the undeveloped seed is usually a small scar on one side of the endocarp. The fruits are oval and usually symmetrical with the single seed filling the entire locule of the pericarp; the undeveloped ovule, however, does not cause the fruit to be asymmetrical as one often finds to be the case in *Psychotria.* In *Faramea* the terminally depressed fruit is the most diagnostic feature of the genus. The ventral funiculus and deeply sulcate endosperm in the single horizontal seed readily distinguish the genus. Mueller's (loc. cit.) description of the seed as "semen torsione ovulo fertilis horizontale, embryo spurie lateralis," is very accurate. Seed coat studies now in progress by the junior author confirm

Table 2. Comparison of *Faramea* and *Coussarea* (distinguishing characteristics only).

Character	COUSSAREA (based on 41 sp.)	FARAMEA (based on 28 sp.)
Stipules	Short, ±5 mm, obtuse, or semi-orbicular	[1]Long sheath—43% ovate, long aristate—52%
Inflorescence	Panicles or pedunculate umbels; usually many flowers	Panicles, fasciate or pedunculate umbels; few flowered
Bracts	Absent or very small	Absent, very small, or rarely large and petaloid
Flowers	Generally white; apex of bud rounded or truncate—90%	Often blue; bud apex acute 88.5%
Corolla	Tube usually elongate with very narrow lobes —78.5%	Lobes usually wider than the tube—82.6%
Style	Bifid; two filamentous lobes	Bifid; two filamentous or clavate lobes
Ovary	Two-locular with two erect ovules, connate by means of the very thin evanescent septum	Two-locular becoming one-locular with two ovules collateral or connate at the apex of the incomplete septum
Fruit	Upright oval drupe; one-seeded by abortion; seed vertical, usually smooth, sometimes tricate; obscure remainder of second seed	Depressed oval drupe; one-seeded by fusion of ovules; seed horizontal; endosperm deeply sulcate ventrally

[1] Styles not observable in 5% of species examined.

the distinctness of the two tribes. Both *Coussarea* and *Faramea* have testa cells with thick walls and definite reticulations as well as large pits visible in the unstained testa. Genera of the *Psychotrieae* examined thus far, viz. *Psychotria, Cephaelis, Palicourea,* and *Rudgea,* have much less thickened cell walls and lack the reticulation pattern of *Coussarea* and *Faramea.* Pits have been found only in *Palicourea.*

Noteworthy also is the striking contrast in flower color; *Coussarea* having white blossoms and *Faramea* blue. Table 2 provides a list of characters which distinguish the two genera based on a study of 69 New World species.

On the basis of the structure of the inflorescence Schumann (loc. cit) distinguished six sections in *Coussarea.* While there is no attempt to emphasize these sections in this limited treatment of the Panamanian species, it is appropriate to point out that *Coussarea enneantha* Standley and *C. villosula* Dwyer, characterized

by a loose pendent dischasium, fall into the section *Laxiflorae,* while *C. paniculata* (Vahl) Standley and *C. impetiolaris* Donn. Smith are characteristic of the section *Paniculatae.* The new species, *C. cerroazulensis* Dwyer, by virtue of its unusual inflorescence, will probably be segregated in a new section when adequate flowering material is available.

The genus *Coussarea* ranges from Mexico, south to the limits of tropical America, with one species in the West Indies. The *Index Kewensis* lists some 100 binomials for the genus with the majority of the species in Brazil. The Panamanian species number at least eight with several being transferred to the new rubiaceous genus *Dukea* Dwyer (Ann. Missouri Bot. Gard. **53:** 360-367, 1966).

Panamanian Species of Coussarea

a. Leaves widely elliptic to elliptic-rotund, 6-25 cm wide, chartaceous to subcoriaceous, the principal veins prominent beneath .... 1. *C. latifolia*

aa. Leaves lanceolate to elliptic, up to 8 cm wide, papyraceous to stiffly chartaceous, the principal veins prominulous beneath (except prominent in *C. cerroazulensis*).

- b. Inflorescence contracted, at maturity less than 3 cm wide.
  - c. Leaves narrowly lanceolate, the acumen 3-4 mm wide in the middle, stiffly papyraceous, the secondary veins 15-20; buds acute, densely pubescent; calyx ovate to elliptic, longer than wide; Darien .... 2. *C. villosula*
  - cc. Leaves elliptic, the acumen 1-2 mm wide in the middle, the secondary veins up to 10; buds obtuse at the apex, glabrous to glabrescent; calyx wider than long; Bocas del Toro .... 3. *C. talamancana*
- bb. Inflorescences patulous, 4-6 cm wide.
  - d. Inflorescence as wide as long, up to 5 cm long.
    - e. Secondary branches of inflorescences capillaceous, ca 1 mm wide; fruits lacking a calyx or with a vague ring at the apex .... 4. *C. darienensis*
    - ee. Pedicels of secondary branches of inflorescence more than 1.5 mm wide at base; fruit capped by an obvious cylindrical calyx.
      - f. Leaves papyraceous, glabrous to glabrescent beneath.
        - g. Leaves petiolate; flowers up to 3.5 cm long; calyx wider than the base of the corolla tube, the teeth 4-8 mm long; corolla with the lobes twice the length of the tube .... 5. *C. enneantha*
        - gg. Leaves sessile or subpetiolate; flowers up to 2.5 cm long; calyx about the same width as the corolla tube, the teeth scarcely measureable; corolla lobes shorter than the tube .... 6. *C. impetiolaris*
      - ff. Leaves very stiffly papyraceous, velutinous-pubescent beneath; fruits 1.5-1.7 cm long, the usually persistent calycine tube about ½ the length of the pericarp .... 7. *C. cerroazulensis*
  - dd. Inflorescence longer than wide, up to 7 cm long .... 8. *C. paniculata*

1. Coussarea latifolia Standley, Jour. Wash. Acad. Sci. **18:** 281, 1928. (Type *Tonduz 9574*)

Known only from Costa Rica and Panama.

Costa Rica. Talamanca, Tsaki, 200 m elev, *Tonduz 9574* (C, F photo). Panama. bocas del toro: Fish Creek Hills, vic Chiriqui Lagoon, *von Wedel 2218* (MO), *2463* (MO).

2. COUSSAREA VILLOSULA Dwyer, Ann. Missouri Bot. Gard. **53:** 105, 1966. (Type *Duke* 5338)

Known only from the type collection in Panama.

DARIEN: Cerro Pirre, S El Real, 750-1030 m elev. *Duke* 5338 (MO).

3. COUSSAREA TALAMANCANA Standley, Publ. Field Mus. Nat. Hist., Bot. Ser., **18:** 1288, 1938. (Type *G. P. Cooper T4*).

Known from Costa Rica and Panama.

COSTA RICA. TALAMANCANA: Talamanca Valley. *Cooper T4* (F). PANAMA. BOCAS DEL TORO: vic Chiriqui Lagoon, *von Wedel 1098* (MO).

Both collections are in bud only. The calyx of *von Wedel 1098* is only about 1 mm long and is actually wider than long. Standley describes the type as "fere 2 mm longo".

4. COUSSAREA DARIENENSIS Steyermark, Ceiba **3:** 20, 1940. (Type *Allen 4576*)

Known from Bocas del Toro and Darien, Panama.

BOCAS DEL TORO: Río Changuinola, vic Surusuba, *Dwyer 4452* (MO); DARIEN: Río Chico, vic Yavisa, *Allen 4576* (F).

Despite the fact that the two collections are at opposite ends of the Republic I regard them as conspecific. My collection, a tree 20 feet tall, while in fruit only has the slender branches of the inflorescence characterizing the type as well as membranaceous few-veined leaves. As the Allen collection lacks fruits, it is appropriate to describe those of the Bocas del Toro collection despite their immaturity: fruit elliptic, ca 0.7 cm long and 0.4 cm wide, obtuse, the style base and/or calycine ring lacking, or merely a lateral ring, glabrous, monospermate, shiny black when dry, yellow when fresh, the pericarp wall ca 0.2 mm thick.

5. COUSSAREA ENNEANTHA Standley, Jour. Wash. Acad. Sci. **18:** 282, 1928. (Type *Williams 841*)

Known only from Darien, Panama.

DARIEN: Cana-Cusai Trail (Camp 2), Chepigana District, 300 ft alt, *Terry 1476* (MO); Cana, *Williams 841* (F photo).

6. COUSSAREA IMPETIOLARIS Donn. Sm., Bot. Gaz. **37:** 418, 1904. (Type *Pittier* 7582)

Known from British Honduras to Panama.

CANAL ZONE: Rd. C-19, Pacific side, *Blum 1901* (MO); K-6 Rd, *Dwyer* 2853 (MO); Barro Colorado Island: *Ebinger 171* (MO), *610* (MO); *Hayden 34* (MO); *Shattuck 621* (MO); vic Río Cocoli, *Stern et al. 324* (MO); Boy Scout Camp entrance, Madden Dam, *Hayden 74* (MO); *Dwyer & Hayden 8* (MO). DARIEN: hill nr Río Chucunaque, ca 4 mi below Yaviza, *Duke 4875* (MO); Cerro Pidiaque, *Duke 8085* (MO); mouth Río Lara, *Tyson & Loftin 3851* (MO). PANAMA: Arraijan, *Woodson et al, 774* (MO).

The white flowers are often quite fragrant. The mature fruits are a waxy white drupe. The common name is "Huecito" (*Duke 8085*).

7. Coussarea **cerroazulensis** Dwyer, sp. nov.

Arbores ad 10 m altae, ramulis teretibus dense villosulis. *Folia* petiolis 2-2.5 cm longis, dense puberulis; stipulae non visae; lamina elliptica, ad 21 cm longa, ad 8 cm lata, apice acuta et conspicue acuminata, acumine gracili, ad 1.5 cm longo, crasso-papyracea dense auropuberula infra praecipue puberula, venis lateralibus late arcuatis ca 12 infra prominentibus dense auro-pubescentibus. *Inflorescentiae* sessiles terminales, ad 5 cm longae, ad 6 cm latae, pedunculo ad 2.5 longo, ca 0.25 cm lato, lignoso, dense pubescente, floribus basalibus geminatis sessilibus in axillis infimorum ramorum, floribus reliquis sessilibus in 3 superioribus ramis, ad 0.5 cm longis, lignosis dispositis. *Flores* calyce (hic in fructu juvenili) persistente terminale cylindrico, ad 0.5 cm longo, ad 0.3 cm lato, coriaceo, pubescente, margine undulato, dentibus nullis. *Fructus* globosi, ad 1.2 cm longi, calyce coronario cylindrico, ad 0.7 cm longo, ad 0.4 cm lato, pericarpio 2-3 mm crasso, superficie dense piloso, semine solitario.

Known only from the Province of Panama, Panama.

PANAMA: Cerro Azul, *Blum, Duke & Odum 2270* (holotype MO); 600 m alt, *Dwyer 1368* (MO).

The two collections were made in the fruiting stage with the persistent calyx evident. The most basally located calyces of *Dwyer 1368* bear pistils which are probably teratological as the hypanthium with its ovary failed to expand, while the persistent style, unbranched for 0.8 cm, bifurcates at the stigmatic position into two foliose lobes; these are oblong, up to 3.5 cm long and 1 cm wide and puberulent with a foliar venation. In all specimens at MO the teratological flowers are sessile and are situated in the axils of the lowermost pair of branches. The sessile inflorescence is extraordinary for *Coussarea*. The fruits appear normal and match those of the type very closely; in both collections they are globose and hairy which is unusual for the genus. These are green in the fresh state with the solitary seed translucent and embedded in a yellow pulp. The ovules apparently unite to form a single seed, thus accounting for the partition-like scar on the endocarp and the globose fruits. These are exceptional characters (cf. Table 2).

8. Coussarea paniculata (Vahl) Standley, Jour. Wash. Acad. Sci. **18:** 282, 1928.

Froelichia paniculata Vahl, Ecol. Am. Praef. 3, 1796; non Moenchner, Method. 50, 1794.
Billardieria paniculata Vahl, Ecol. Am. Praef. 10, 1796.
Coussarea froelichia A. Rich., Mém. Soc. Hist. Nat. Paris **5:** 177, 1834.

Known from Panama, Trinidad, and northern South America.

DARIEN: Puerto St. Dorothea, *Dwyer 2222* (MO).

NOTES

THE GENUS POINSETTIA (EUPHORBIACEAE) IN FLORIDA

Dressler's publication in 1962 (Ann. Missouri Bot. Gard. **48:** 329-341) of a synopsis of the genus *Poinsettia* did much to unravel the synonymy of a group which had long been in need of critical study. Most of his field work was done in Central America and the southwestern United States, but an examination of Florida material suggests that in most cases his conclusions hold well for collections from that State. The one exception is his reduction to synonymy of Small's *Poinsettia pinetorum*, which is understandable in that the name has largely been misapplied on material in the herbaria which he examined, but which is easily seen to be a mistake when collections from the pinelands of southern Florida are available.

The following key will separate the species known to occur or which may be found in the State:

1a. Plants woody, often more than 2 m tall; cyathium more than 5 mm diam; seed ca 10 mm long ..... *P. pulcherrima*

1b. Plants herbaceous or ligneous at base, but rarely reaching 1 m tall; cyathium 2-3 mm diam; seed ca 3 mm long.

- 2a. Plants perennial from thickened storage roots; leaves all linear, floral bracts and upper leaves sometimes flushed deep purple; cyathia deep purple, rarely more than 5 in a cluster, glands bilabiate, usually 4 per cyathium ..... *P. pinetorum*
- 2b. Plants annual or perennating, but rootstocks not markedly enlarged for storage; leaves often broad, pandurate or ovate, rarely narrower than linear-lanceolate; floral bracts green, purple spotted or white or red flushed at base but not uniformly deep purple; cyathia green, usually in clusters of 5-20, glands bilabiate or cup-shaped, rarely more than one except in the first cyathium formed in a cluster.
  - 3a. Cyathial gland with a circular opening; floral bracts green or purple spotted, but never red at base; seed angular ..... *P. heterophylla*
  - 3b. Cyathial gland bilabiate; floral bracts green or red at base; seed not angular.
    - 4a. Plants glabrous or with soft pubescence at tips; lower leaves alternate; floral bracts usually red at base ..... *P. cyathophora*
    - 4b. Plants usually hispid-pubescent, particularly at tips; leaves opposite or rarely subopposite; floral bracts green, often white near base ..... *P. dentata*

Poinsettia pulcherrima (Willd.) Grah.

Commonly cultivated as an ornamental in peninsular Florida, and to be expected as an escape or as plants persisting on the sites of old homesteads in the southern part of the State.

Poinsettia pinetorum Small

This species resembles the most extreme narrow-leaved forms of *P. cyathophora*, but it may be distinguished by the multiple glands of most of its cyathia, by the

Ann. Missouri Bot. Gard. **53:** 375-384, 1966.

deep purple color of the cyathia and upper leaves, and by the swollen perennial rootstock. It has been found only in the pinelands of the oölitic limestone of Dade and Monroe counties, and forms part of the rich flora of this habitat threatened by man's activity in farming, building houses and preventing fires.

Poinsettia heterophylla (L.) Kl. & Gke.

Dressler points out that most workers have made no distinction between two easily separable species of American plants when using the name *Euphorbia heterophylla* L. An examination of a wide range of herbarium material confirms that the name has been applied both to the annual poinsettia with red and green floral leaves and a bilabiate cyathial gland, and to a coarser species with all leaves green (or at most purple splashed) and a circular mouth to the gland. He suggests that the name should be used for this second species, and that the more familiar plant with red coloration in its leaves should be called *E. cyathophora* Murr. [= *Poinsettia cyathophora* (Murr.) Kl. & Gke.]. His justification of this is a little terse, but the conclusion appears to be sound and will be followed here.

This plant of disturbed areas is common through the West Indies, Central and tropical South America. It appears to be quite widespread in peninsular Florida, but has probably been overlooked by most collectors in favor of the showier red-leafed species.

Poinsettia cyathophora (Murr.) Kl. & Gke.

Both this and the preceding species show a great deal of plasticity in their leaf shape, and the extremes of broad and linear leaves, which have been considered to belong to distinct taxa by some authors, often occur in the same population or even on different parts of the plant.

This species is found throughout Florida and in much of the eastern, southern and southwestern United States. Its range matches that of *P. heterophylla* in Central America and the West Indies, but it is of much less common occurrence in South America.

Poinsettia dentata (Michx.) Kl. & Gke.

No collection of this northern weed is known from the State, but it is included here since it seems possible that the southern limit of its range might include northern Florida as reported by Small in his *Manual of the Southeastern Flora*.—*Derek Burch, Missouri Botanical Garden, St. Louis.*

ILEX DISCOLOR VAR. LAMPROPHYLLA (STANDL.) EDWIN, STAT. NOV. (AQUIFOLIACEAE)

Ilex discolor Hemsl. var. **lamprophylla** (Standl.) Edwin, stat. nov., based on *I. lamprophylla* Standl., Jour. Wash. Acad. Sci. **15:** 476, 1925; *I. carpenterae* Standl., loc. cit. 477; *I. davidsoniae* Standl., Field Mus. Nat. Hist., Bot. Ser., **22:** 88, 1940—*Gabriel Edwin, Field Museum of Natural History, Chicago, Illinois.*

A NEW SPECIES OF INGA (LEGUMINOSAE) FROM PANAMA

Inga tysonii Elias, sp. nov.

Arbor ad 10 m alta; rami et ramuli teretes, glabri, lenticellati. *Folia* foliolarum 1-2 jugis; petiolus 1.4-2 cm longus, glaber, anguste alatus, nigrescens basi; rhachis 3-5 cm longa, glabra, anguste alata, ala truncata, usque ad 5 mm lata, glabra supra subterque; stipulae caducae, non visae; glandulae rhachidis usque ad 1 mm diametro, sessiles, marginibus angustis; foliola 8.5-15 cm longa, 3.5-5 cm lata, elliptica vel oblongo-elliptica, brevi-acuminata vel anguste acuta ad apicem, cuneata ad basim, glabra supra subterque, lateralium venarum 5-8 jugis, inconspicuarum, petiolulis 1.5-3 mm longis, glabris, nigrescentibus maturitate. *Inflorescentiae* spicatae, ad 3-4 cm longae, in axillis superioribus dispositae, multiflorae; bracteae anguste lanceolatae, usque ad 1 mm longae, parce villosae; gemmae non visae; pedunculus ad 5 mm longus, parce villosus; calyx .75-1 mm longis, campanulatus, parce villosus, sessilis, lobis ad 0.5 mm longis, ovatis; corolla 3-4 mm longa, tubulosa, leviter dilata ad apicem, parce villosa, lobis ad 0.5 mm longis, ovatis; tubus staminalis exsertus ad 2-2.5 mm; filamenta alba, ad 1 cm longa, antherae dorsifixae; pistillum ad 1 cm longum. *Legumen* ignotum.

CANAL ZONE: rd from Fort Sherman to Gatun Locks, *Tyson & Blum 3803* (holotype MO); hills SW of Gatun, *Johnston 1691* (MO).

A flattened legume is suspected because of the nature of the flowers and the affinities for species with flattened fruits. *Inga tysonii* can be distinguished by the short congested inflorescence and a short peduncle. Its affinities are with *I. marginata* which has similar foliar characters but possesses a long, laxly flowered inflorescence.—*Thomas S. Elias, St. Louis University, St. Louis, Missouri.*

TYPIFICATION OF HEDYOTIS PROCUMBENS (RUBIACEAE) AND A NEW VARIETY FROM SOUTHEASTERN UNITED STATES

Hedyotis procumbens (J. F. Gmel.) Fosberg, Castanea **19:** 32, 1954, is based on *Poiretia procumbens* J. F. Gmel. in L., Syst. Nat., ed. 13, **2:** 263, 1791, and *Anonymos procumbens* Walt., Fl. Carol. 86, 1788, nom. illegit. No specimen of the species exists in Walter's herbarium housed at the British Museum and presumably is not extant. Walter's collections were made within a 50 mile radius of his plantation in (now) Berkeley Co, South Carolina, and his Flora was based largely on these and those made by Fraser in neighboring Charleston. Since the species is rare in that State and presently is known from only Beaufort, Charleston and Colleton Counties (Radford et al., *Guide Vasc. Fl. Carol.* 803, 1964), I have selected the neotype from among material of that area. Apparently the collection(s) used by Walter as a basis of *Anonymos procumbens* was not from Berkeley Co, where the species remains unknown, but rather that collected by Fraser in Charleston where the species is found, though rarely. The only specimen in the U.S. Na-

tional Herbarium from that county is the more common glabrous leafed variety which is designated neotype: *Wm. Palmer* s.n., 2-10 June, 1902; SOUTH CAROLINA: Charleston Co., Charleston (US, 513671).

Hedyotis procumbens var. **hirsuta** W. H. Lewis, var. nov. Differt a var. *procumbens* foliis hirsutis supra et capsulis hirsutis. Type: *Sidney McDaniel 4707*, 28 May 1964; FLORIDA: Walton Co, Villa Tasso, 1 mi W of Choctaw Bay (holotype FSU).

a. Capsules and upper leaf surfaces glabrous or occasionally slightly hirsute especially leaf margins and young leaves .... var. *procumbens*
aa. Capsules and upper leaf surfaces hirsute .... var. *hirsuta*

Known from the coastal plain of Florida, Georgia, Alabama, Mississippi and Louisiana; often growing with the typical variety which is also found infrequently in South Carolina and in the southern Appalachian Mts if the following locality is reliable, viz. "Thunderhead Mt [Sevier Co], E Tennessee," *A. Ruth s.n.*, June 1891 FSU).

Representative specimens of var. *hirsuta:*

ALABAMA: Mobile Co, Mobile, *Mohr s.n.* (US), nr Mobile, *Drushel s.n.* (MO). FLORIDA: Duval Co, nr Jacksonville, *Curtiss 4521* (US), S Jacksonville, *Churchill 752* (MO), nr Jacksonville, *Curtiss 1141* (MO, US) (with var. *procumbens*), ca 4 mi E of Eastport, *Moldenke 174* (MO); Franklin Co, Apalachicola, Biltmore Herb 3973a (US) (with var. *procumbens*); Jefferson Co, Monticello, *Lighthipe s.n.* (MO) (with var. *procumbens*); Lake Co, vic of Eustis, *Nash 1291* (MO, US); Orange Co, Clarcona, *Meislahn 160* (US); Polk Co, *Milligan s.n.* (US); Washington Co, 3 mi S of Chipley, *Kral 1926* (FSU) (with var. *procumbens*); Mellonville, *Coulter 2774* (MO). GEORGIA: Sumter Co, *Harper 454* (US). LOUISIANA: St Tammany Par, vic of Covington, *Arsène 11938* (US). MISSISSIPPI: Greene Co, 4.6 miles NE of Leaksville, *Lewis 5136* (MO); Jackson Co, Ocean Springs, *Skehan s.n.* (MO) (with var. *procumbens*).

—*Walter H. Lewis, Missouri Botanical Garden, St. Louis.*

THREE LOST SPECIES OF PIPER (PIPERACEAE)

Paul C. Standley described as new three species of *Piper* from Panama (Publ. Field Mus. Nat. Hist., Bot. Ser., **22:** 135-137, 1940) which were not mentioned by T. G. Yuncker in the *Piperaceae* of the *Flora of Panama* (Ann. Missouri Bot. Gard. **37:** 1-22, 1950). A thorough search of the latter revealed that *Terry & Terry 1461*, the type collection of one of Standley's new species, is cited under a species described as new by Yuncker. From this evidence and from close inspection of the descriptions of both species it would appear that the two are identical and that the correct name on the basis of priority must be that supplied by Standley. None of the other Terry & Terry collections cited as types by Standley is mentioned by Yuncker. It is apparent that Yuncker overlooked Standley's publication and since Yuncker did not examine material at the Chicago Natural History Museum (F) for the *Flora of Panama* he thus missed discovering the type materials. Although disposition of Standley's names is beyond the scope of this note, a list is given below since they do not occur in *Flora of Panama* and might otherwise continue to be overlooked.

Piper canaense Standl., Publ. Field Mus. Nat. Hist., Bot. Ser., **22:** 135, 1940. Type: PANAMA. DARIEN: Cana-Cuasi trail, *Terry & Terry 1461* (holotype F, isotype MO).

Piper hastularum Yuncker, Ann. Missouri Bot. Gard. **37:** 21, 1950. Type: COLOMBIA. CHOCÓ: Bahio Solana, *Killip & Garcia* 33568 (US).

Piper cuasianum Standl., Publ. Field Mus. Nat. Hist., Bot. Ser., **22:** 136, 1940. Type: PANAMA. DARIEN: Cana-Cuasi trail, *Terry & Terry 1531* (F).

Piper terryae Standl., Publ. Field Mus. Nat. Hist., Bot. Ser., **22:** 136, 1940. Type: PANAMA. DARIEN: Cana-Cuasi trail, *Terry & Terry 1459* (F).—*Sidney McDaniel, The Florida State University, Tallahassee, Florida.*

NEW PIPERACEAE FROM ECUADOR

Piper **dodsonii** Yuncker, sp. nov.

Frutex ramosus nodosus, internodiis superis gracilibus plus minusve striatis strigosis deorsum glabrecentibus; *foliis* ellipticis apice acute-acuminatis basi subaequilateraliter acutis supra hispidulo-scarbridis subtus hispidulis pilis adpressis plus minusve ciliolatis glanduloso-punctatis ad mediam laminam pinnatim venosis, nerviis utrinque 4, petiolo strigoso ad basim vagnato-alato, pedunculo gracile hispido, bracteis arcte triangulari-subpeltatis fimbriatis, ovario ovoideo breviter styloso, stigmatibus linearibus, drupa matura non visa.

Freely branching, nodose *shrub;* upper internodes slender, 2-3 cm long above, abruptly lengthening toward the base, somewhat striate and green when dry, strigose above, glabrescent toward the base, the hairs white, upwardly appressed, about 0.3 mm long. *Leaves* elliptic, with sharp-acuminate apex and subequilaterally acute base, 2-3 cm wide and 5.5-7 cm long, hispidulous-subscabrid above, the hairs appressed, hispidulous beneath with the nerves more densely so, the hairs appressed, more or less ciliolate, pinnately nerved to about the middle, the nerves 4 on each side, with cross-connecting, anastomosing nervules, pale glandular-dotted, drying chartaceous, translucent; petiole 5-10 mm long, strigose, vaginate winged at the base. *Spikes* 2-2.5 mm thick and 1-1.5 cm long; peduncle 10-13 mm long, slender, hispid; bracts narrowly triangular-subpeltate, fringed; stamens 4; ovary ovoid, with pointed apex and very short, stout style, the stigmas linear; mature drupes not seen.

ECUADOR. LOJA: 12-14 km, rd to Zamora, nr top of pass; wet, windy, cold, alt 2800 m, 28 Sept 1961, *Dodson & Thien* 797 (holotypus MO, isotypus DPU).

The slender, strigose branches, small, hispid, 4-nerved leaves, small spikes, and somewhat stylose ovaries are distinctive characters of this species.

Piper **nebuligaudens** Yuncker, sp. nov.

Frutex ramosus nodosus, internodiis superis gracilibus conferte brunneo-villosis; *foliis* ellipticis apice brevi-acuminatis basi subaequilateralibus latere uno 1-2 mm breviore acutis latere longiore acutis ad subobtusis utrinque conferte pubescentibus,

pilis pro more erectis, totis conferte ciliatis a medio infero pinnatim venosis, nerviis utrinque 5, pellucido-punctatis, petiolo conferte pubescente ad basim vaginato; *spicis* rectis, bracteis triangulari-subpeltatis fimbriatis pedicello piloso, drupa globoso-ovoidea glabra, stigmatibus sessilibus.

Branching, nodose *shrub*, 1-1.5 m high; upper internodes slender, 2-4 cm long, lengthening downward, densely brown-villous, the hairs 0.5-1 mm long. *Leaves* elliptic, with short-acuminate apex, the base subequilateral, one side 1-2 mm shorter at the petiole and acute, the longer side acute to subobtuse, densely pubescent on both sides, the nerves more densely so, the hairs mostly erect, densely short-ciliate throughout, 2.5-4 cm wide and 5-9.5 cm long, pinnately nerved from the lower half, the nerves 5 on each side, with cross-connecting, anastomosing nervules, drying chartaceous, finely pellucid-dotted; petiole 5-10 mm long, densely pubescent, vaginate at the base. *Spikes* straight, 2 mm thick and up to 3 cm long; peduncle less than 1 cm long, pubescent; bracts triangular-subpeltate, fringed, the pedicel pilose; stamens 3; drupe globose-ovoid, glabrous, the stigmas sessile.

Ecuador. cañar: tropical cloud forest, km no. 110 from Duran, alt 1300 m, 15 Jan 1962, *Dodson & Thien 2120* (holotypus MO, isotypus DPU).

The dense pubescence, comparatively small leaves, and rather small spikes are distinctive characters of this species. It resembles *P. mollicomum* Kunth in the character of its pubescence but differs in the size and shape of the leaves, and much smaller, straight spikes. It also is close to *P. cimborazoense* Yuncker but differs in the denser pubescence, hairs on the midrib beneath erect rather than appressed, shorter peduncles, and shorter spikes. The name refers to its cloud-forest habitat.

Sarcorhachis sydowii Trel. var. **hirsuta** Yuncker, var. nov.

Plus minusve pubescente.

Differing from var. *sydowii* in that the young branches, petioles, and lower leaf surface toward the base are more or less pubescent.

Ecuador: zamora: rd from Loja to Zamora, km 45-51, alt 1400-1600 m, 20 Nov 1961, *Dodson & Thien 1423* (holotypus MO; isotypus DPU).

Peperomia **thienii** Yuncker, sp. nov.

Herba repenti-adsurgens glabra; *foliis* alternis elliptico-subovatis apice acuminatis basi acutis in infima parte laminae ad 1 cm 7-plinervis costa venisque seorsum bene ramosis eciliatis; *spicis* terminalibus axillaribusque, bracteis rotundato-peltatis, drupa globoso-ovoidea apice obliquo-acuminata, stigmate subapicali.

Repent, assurgent, glabrous *herb;* stem 4-5 mm thick when dry, the internodes 1.5-3 cm or more long. *Leaves* alternate, elliptic-subovate, with acuminate apex and acute base, 3-4.5 cm wide and 5-7.5 cm long, 7-plinerved within the lowermost 1 cm, the midrib and nerves much branched upward, eciliate or sparsely ciliolate near the apex, pale glandular-dotted, drying subcoriaceous, translucent; petiole 5-10 mm long. *Spikes* terminal and axillary, 3 mm thick and up to 12 or 15 cm long; peduncle scarcely 1 cm long; bracts round-peltate, the margin somewhat irregular; drupe globose-ovoid, with obliquely pointed apex and subapical stigma.

Ecuador. Guayumo on rd from Quito to Nanegal, alt 2000 m, 26 Oct 1961, *Dodson & Thien 1112* (holotypus MO).

The glabrous, alternate, rather large, plinerved leaves, scarcely twice longer than wide, comparatively large spikes, and obliquely acute drupes are distinctive characters of this species. It belongs in the subgenus *Sphaerocarpidium* near *P. guaiquinimana Trel. & Yuncker* from which it differs, however, in its larger leaves, larger spikes, and other characters.—*T. G. Yunker, DePauw University, Greencastle, Indiana* (posthumously).

NEW SPECIES OF PIPER AND PEPEROMIA (PIPERACEAE) FROM PERU

Piper **mazamariense** Yuncker, sp. nov.

Arbor 8-metralis nodosa, internodiis superis conferte villosis deorsum glabrescentibus pilis erectis; *foliis* oblongo- vel lanceolato-ellipticis apice breviter acuminatis basi valde inaequlateraliter cordato-aurculatis lobo majore petiolum obtegente supra costam ad basim dissite hirsutis subtus ad costam et venas hirtulo-villosis totis pinnatim venosis nervis ca 10 + 13 vel 14, petiolo ad laminam vaginato-alato hirtello-villoso, bracteis conchiformis ad apicem subtriangularibus margine infero brevi-fimbriatis, drupa oblonga latere compressa apice truncata brunneo-puberula.

Nodose *tree,* 8 m high; uppermost internodes 4-6 cm long, densely villous with an inconspicuous minutely hirtellous understory glabrescent downward, the hairs essentially erect, 1 mm or more long, tawny. *Leaves,* oblong- or lance-elliptic, with short-acuminate apex and strongly inequilaterally cordate-auriculate base, the longer lobe equalling or surpassing and covering the petiole, peltate 5-15 mm from the margin, thinly hirsute above along the midrib near the base, minutely hirtellous along the midrib and major nerves beneath, with a mixture of long hairs up to 1 mm long on the midrib and nerves toward the base, pinnately nerved throughout, the nerves about 10 on each side + 3-4 additional shorter ones descending in the longer lobe, with shorter intermediates and slender, cross-connecting, anastomosing nervules, finely venulose by transmitted light, 13-18 cm wide and 25-30 cm long, drying firm, chartaceous, translucent; petiole 5-6 cm long, vaginate-winged to the blade, hirtellous-villous. *Spikes* 5 mm thick and 15 cm or more long when mature, the peduncle 2-2.5 cm long, comparatively slender, thinly pubescent glabrescent, the bracts conchiform, subtriangular at the top, narrowly fringed, especially along the lower margin, the drupe oblong, laterally flattened by pressure, with truncate, densely brown-puberulent apex, and with 3, slender, recurved stigmas.

Peru. junin: Mazamari, in shady forest, alt 800 m, 2 Sept 1960, *Woytkowski 5935* (holotypus MO).

The large, tree-like plants, with large cordate-auriculate, narrowly-peltate leaves, and hirtellous drupes are distinctive features of this species.

Piper **subbrunneispicum** Yuncker, sp. nov.

Frutex; internodis superis dissite gracili-pilosis ciliis rectis ca 1 mm longis, pilis brevioribus densioribus; *foliis* rhombeo-ellipticis apice anguste vix falcatis acuminatisque basi inaequilateraliter latere altero 3-5 mm breviore latere longiore auriculato petiolum obtegente supra dissite pilosis pilis albo-flaccidis subtus dissite longepilosis pilis ad costam brevioribus longioribusque una intermixtis subciliatis ad medium laminam pinnatim venosis, nervis 5 + 6, petiolo dissite piloso ad medium vaginato; *spicis* brevi-apiculatis, bracteis trangulari-subpeltatis margine papillatis, ovario globoso-ovoideo apiculato, stigmatibus 2, linearibus.

Shrub, 1.5 m or more high; upper internodes 2.5-3 cm or more long, thinly long-pilose, the hairs erect, 1 mm or more long, with a more dense puberulous understory. *Leaves* rhombic-elliptic, with attenuately and narrowly, somewhat falcately, sharp-acuminate apex, the base strongly inequilateral, one side 3-5 mm shorter at the petiole, narrowly rounded and obtuse, the longer side auriculate and longer than and covering the petiole, (8-) 9-10 cm wide and 20-23 cm long, thinly pilose above with white flaccid hairs up to 1 mm long, loosely long-villous beneath along the midrib and major nerves, the hairs becoming much shorter toward the margin, the midrib with a puberulous understory, the margin subciliate with occasional distant hairs, pinnately nerved to about the middle, the midrib up to 5 mm nearer the shorter side, the nerves 5 + 6, with slender, cross-connecting, anastomosing nervules, finely glandular-dotted, drying thin, translucent; petiole 3-5 + 3-5 mm long, loosely pilose, vaginate to the middle. *Spikes* 3 mm thick and 8 cm long, short-apiculate, reddish-brown when growing, the peduncle 1 cm long glabrescent, the bracts triangular-subpeltate, narrowly papillate fringed, the broad pedicel villous; stamens 3; ovary globose-ovoid, apiculate, with 2, linear, recurved stigmas.

PERU. SAN MARTIN: Río Negro, in shady forest, alt 1000 m, 12 Jan 1961, *Woytkowski 6187* (holotypus MO).

The type of pubescence, leaf shape and size, subglabrous bracts, and apiculate ovary with two stigmas are distinguishing characters of this species. It resembles *P. achupallasense* of Ecuador to some extent but differs in its more auriculate leaf base, thinner pubescence, fewer nerves, etc.

Piper **cajamarcanum** Yuncker, sp. nov.

Frutex, internodiis superis conferte albido-pubescentibus; *foliis* late plus minusve oblique ovatis apice acuminatis basi inaequilateralibus latere altero ad petiolum usque ad 5 mm brevore rotundato-obtusis latere longiore rotundato-obtusis vel subcordatis supra hispido-scabridis subtus velutino-pubescentibus proxime laminam mediam pinnatim venosis, nerviis utrinque 7-8, petiole conferte pubescente ad basim vaginato; *spicis* apiculatis, pedunculo conferte pubescente, bracteis triangulari-subpeltatis breviter fimbriatis, drupa oblonga angulata glabra, stigmatibus linearibus sessilibus.

Shrub, 6 m high; upper internodes 3.5-6 cm or more long, densely white-pubes-

cent, the hairs ca 0.5 mm long, erect to reflexed. *Leaves* broadly somewhat obliquely ovate, with acuminate apex and rounded inequilateral base, one side up to 5 mm shorter at the petiole, rounded, obtuse, the longer side rounded, obtuse or subcordate, hispid and scabrid above, velvety pubescent beneath, ciliate, 6-12 cm wide and 12-20 cm long, pinnately nerved from below the middle, the nerves 7-8 on each side, with cross-connecting, anastomosing nervules, drying green above, paler beneath, chartaceous, translucent; petiole about 15 + 5 mm long, densely pubescent, vaginate at the base. *Spikes* straight, apiculate, 4-5 mm thick and 8-10 cm long; peduncle 1-1.5 cm long, densely pubescent; bracts triangular-subpeltate, narrowly fringed; stamens 4; drupe oblong, angular, glabrous, the apex truncate or subconvex, the stigmas linear, sessile.

PERU. CAJAMARCA: Colasay, Andean low forest, alt 2700 m, 30 Oct 1961, *Woytkowski 7033* (holotypus MO, isotypus DPU).

The densely velvety pubescent parts, ovate, scabrous leaves, comparatively thick spikes and glabrous drupes are distinctive characters of this species.

Piper **pilosissimum** Yuncker, sp. nov.

Frutex, internodiis superis conferte brunneo-villosis, pilis usque ad 1 mm vel ultra longis; *foliis* ellipticis apice acuminatis basi in inaequilateralibus latere quam altero ad petiolum 2-3 mm breviore obtusis ad cordulatis latere longiore cordulato-subauriculatis utrinque villosis ad nerviis pro maxime eciliatis ad mediam laminam pinnatim venosis, nervis utrinque 5-6; *spicis* plus minusve arcuatis, bracteis triangulari-subpeltatis dorsalis longe-piloso, ovario ovoideo bene piloso stylo crasso coronato, stigmatibus linearibus, drupa non visa.

Shrub, up to 2 m high; upper internodes slender, 2-3 cm or more long, densely brown-villous, the hairs 1 mm or more long, erect to subretrorse. *Leaves* elliptic, with acuminate apex and inequilateral base, one side 2-3 mm shorter at the petiole and obtuse to cordulate, the longer side cordulate-subauriculate, pubescent above, the costa densely villous, soft villous beneath, the midrib and nerves densely so with spreading hairs up to 1 mm or more long, scarcely ciliate, 4-5 (-6) cm wide and 10-14 cm long, pinnately nerved to about the middle, the nerves 5-6 on each side, with cross-connecting, anastomosing nervules, drying chartaceous, subopaque; petiole 2-3 + 2-3 mm long, densely villous, vaginate below the middle. *Spikes* gently curved, 3 mm thick and 5 cm long; peduncle 2-2.5 cm long, densely villous; bracts triangular-subpeltate, strongly pilose, the lower angle with several unusually long hairs, the pedicel villous; stamens 6; ovary ovoid, densely pubescent, with short, thick, pilose style and linear stigmas; mature drupes not seen.

PERU. CAJAMARCA: Colassay, alt 2500 m, 30 Oct 1961, very common, wooded shady ravine, leaves always with insect damage, *Woytkowski 6999* (holotypus MO, isotypus DPU).

The strongly villous parts, eciliate leaves, comparatively long peduncles, dorsally long-pilose bracts, and densely pubescent, stylose ovaries are distinctive characters of this species. It resembles *P. transpontiantum* Trel. in the character of the bracts but differs in a number of other characters. The name refers to the densely hairy parts.

Peperomia **woytkowskii** Yunker, sp. nov.

Herba adsurgens terrestris, caule conferte crispo-pubescente, pilis usque ad 0.5 mm longis; *foliis* alternis vel nonnunquam oppositis late ellipticis rotundato-ellipticis vel subobovatis apice rotundatis sub-acutisque basi acutis supra ad costam deorsum pubescentibus subtus glabris ultra medium ciliolatis basi laminae ad 5 mm 9-plinervis; *spicis* terminalibus, bracteis rotundato-peltatis, drupa globoso-ovoidea apice oblique acutata, stigmata subapicali.

Adsurgent to erect, terrestrial *herb,* up to 40 cm high; stem 5 mm thick downward when dry, moderately to densely crisp-pubescent, the hairs up to 0.5 mm long, the internodes 1-3 cm long. *Leaves* alternate or occasionally opposite, broadly elliptic, elliptic-obovate or obovate, with rounded or subacute apex and acute base, crisp-pubescent above along the midrib toward the base, glabrous beneath and wine red when growing, ciliate above the middle, 7-9 plinerved, the nerves coalescing within the lowermost 5 mm, the midrib and lateral nerves branched upward, 2-3.5 (-4.5) cm wide and 4-5 (-6) cm long, glandular-dotted, drying firm, translucent, pellucid-dotted; petiole 1-1.5 cm long. *Spikes* terminal and axillary, reddish-brown when growing, 2 mm thick and 7-11 cm long; peduncle 1 cm long; bracts round-peltate; drupe globose-ovoid, about 0.75 mm long, with obliquely pointed apex and subapical stigma, eventually on pseudopedicel.

PERU. JUNIN: Yaupe, in tall, shady forest, alt 1600 m, 2 July 1961, *Woytkowski 6390* (holotypus MO, isotypus DPU).

The rather densely pubescent stem, broadly elliptic-obovate to obovate, nearly glabrous leaves with obtuse or subacute apex are distinctive characters of this species. It bears some resemblance to *P. rhombilimba* Trel. but differs because of its more obtusely pointed and proportionately wider leaves, and denser stem pubescence.—*T. G. Yuncker, DePauw University, Greencastle, Indiana* (posthumously).

GENERAL INDEX TO VOLUME 53

New names and epithets are printed in **boldface.** Taxa mentioned only incidentally are not indexed. An index to Latin names is included at the end of each article of a monographic nature.

African type collections, photographs of 264

Allomarkgrafia, and Aspidosperma (Apocynaceae), new species of 104-105; **tubiflora** 104

Americas, the Asian genus Neanotis nomen novum (Anotis) and allied taxa in the (Rubiaceae) 32-46

Anotis, Neanotis nomen novum, the Asian genus and allied taxa in the Americas (Rubiaceae) 32-46

Apocynaceae, Mesechites pilosissima Woodson new to Peru 260-261; new species of Allomarkgrafia and Aspidosperma 104-105

Aquifoliaceae, Ilex discolor var. **lamprophylla** (Standley) Edwin 376

Arcytophyllum laricifolium 110

Aristolochia (Aristolochiaceae), revision of the north and central American hexandrous species of 115-196; key to the species 122, human uses 121, morphology 116, taxonomy 122; anguicida 177; arborea 134; asclepiadifolia 138; bilabiata 171; bilobata 145; **bullata** 134; californica 141; **carterae** 178; caudata 172; chapmaniana 182; chasmema 168; clavidenia 152; clematitis 174; constricta 185; ehrenbergiana 173; ekmanii 164; **esoterica** 159; fuertesii 153; gigantea 159; glandulosa 152; **glossa** 180; grandiflora 164; haitiensis 148; inflata 176; labiata 156; leptosticta 147; lindeniana 146; linearifolia 170; littoralis 160; macrophylla 140; malacophylla 132; maxima 166; montana 179; mycteria 181; odoratissima 161; orbicularis 185; ovalifolia 169; panamensis 136; **paracleta** 135; passifloraefolia 155; peltata 146; pilosa 149; reticulata 128; rhizantha 138; ringens 157; rugosa 154; samanensis 166; schippii 175; serpentaria 128; taliscana 151; tentaculata 149; thwaitesii 139; tigrina 165; tomentosa 142; tonduzii 183; trilobata 144; tricaudata 132; veraguensis 174;

Aristolochiaceae, revision of the north and central American hexandrous species of Aristolochia 115-196

Asia, chromosome numbers of Oldenlandia corymbosa (Rubiaceae) from southeastern 257-258

Asian, the genus Neanotis nomen novum (Anotis) and allied taxa in the Americas (Rubiaceae) 32-46

Aspidosperma, and Allomarkgrafia (Apocynaceae) new species of 104-105; **dariense** 104

Bernoullia Oliv., a genus of Bombacaceae new to Panama 112-113

BLECK, JOHN: 1-16

Bombacaceae, Bernoullia Dliv., a genus new to Panama 112-113

BOLD, HAROLD C.: 17-27

BURCH, DEREK: The genus Poinsettia (Euphorbiaceae) in Florida 375-376; Two new species of Chamaesyce (Euphorbiaceae), new combinations, and a key to the Caribbean members of the genus 90-99

Caribbean, two new species of Chamaesyce (Euphorbiaceae), new combinations, and a key to members of the genus 90-99

Central American, and North American, revision of the hexandrous species of Aristolochia 115-196

Central American, and Mexican, revision of Saurauia (Dilleniaceae) 47-89

Central American, and West Indian species of Inga (Leguminosae) 265-359

Chamaesyce, two new species of, new combinations, and a key to the Caribbean members of the genus (Euphorbiaceae) 90-99; key to the Caribbean taxa 91; adenoptera subsp. **gundlachii** 98, subsp. **pergamena** 98; deltoidea subsp. deltoidea var. **adhaerens** 99, subsp. **serpyllum** 99; **helwigii** 98; **hepatica** 98; lecheoides var. **exumensis** 99, var. **wilsonii** 99; **leonardii** 96; **minutula** 98; **opthalmica** 98; **parciflora** 98; porteriana var. **keyensis** 99, var. **scoparia** 99; **tumistyla** 97

Chromosome numbers of phanerogams 1. 100-103

Claytonia rosea and C. lanceolata (Portulacaceae), taxonomic status of 205-212; barriers to gene exchange 208, cytology 206, gross morphology and distribution 205; caroliniana var. **spatulifolia** 258

Cochlospermaceae, the publication date of the genus Cochlospermum 113

Cochlospermum (Cochlospermaceae), the publication date of the genus 113

Compositae pollen, systematic implications from electron microscopic studies—a review 220-256; morphology of Compositae pollen walls 223; pollen wall morphology at tribal level 233; preparation of pollen walls 223

Compsopogon, a preliminary ultrastructural study of the freshwater red alga 17-27; materials and methods 18; observations 18

Convolvulaceae, chromosome number of

100; Convolvulus rozynskii (Standl.) Lewis and Oliver 110
Convolvulus **rozynskii** 110
Coussarea, new species from Panama (Rubiaceae) 105; notes on, especially the Panamanian species (Rubiaceae) 368-374; **cerroazulensis** 374; darienensis 373; enneantha 373; impetiolaris 373; latifolia 372; paniculata 374; talamancana 373; **villosula** 105
Daphniphyllum, two new species of 28-31; glaucescens subsp. **borneense** 31, subsp. **scortechinii** 31; **philippinense** 31; **woodsonianum** 28
Dilleniaceae, revision of Mexican and Central American Suarauia 47-89
Dukea, a new genus of the Rubiaceae (tribe Mussaendeae) 360-367; section **uniloculata** 366; **blumii** 365; **charianthа** 364; **darienensis** 365; **euryphylla** 366; **panamensis** 364; **victoriae** 364
DWYER, JOHN D.: A new species of Platymiscium (Leguminosae) from Panama 105; Dukea, a new genus of the Rubiaceae (tribe Mussaendeae) 360-367; New species of Allomarkgrafia and Aspidosperma (Apocynaceae) 104-105; New species of Coussarea, Machaonia, and Psychotria (Rubiaceae) from Panama 105-106;
DWYER, JOHN D. and SISTER M. VICTORIA HAYDEN: Notes on Coussarea (Rubiaceae), especially the Panamanian species 368-374
Ecuador, new Piperaceae from 379-381
EDWIN, GABRIEL: Ilex discolor var. lamprophylla (Standl.) Edwin (Aquifoliaceae) 376
ELIAS, THOMAS S.: A new species of Inga (Leguminosae) from Panama 377
Erythronium (Liliaceae), the genus in Kansas 197-204; Chromosome numbers and morphology 200; leaf morphology 199; floral morphology 200; fruit morphology 200; systematic treatment 201; vegetative reproduction 200; white-flowered species 197; yellow-flowered species 197; albidum 202; mesochoreum 202; rostratum 201
Euphorbiaceae, the genus Poinsettia in Florida 375-376; Two new species of Chamaesyce, new combinations, and a key to the Caribbean members of the genus 90-99
Florida, the genus Poinsettia (Euphorbiaceae) in 375-376 Gloeospermum, two new species from Panama (Violaceae) 110-111; **ferrugineostictum** 111; **portobelense** 111
HALLECK, DIANNE K.: Taxonomic Status of Claytonia rosea and C. lanceolata (Portulacaceae) 205-212
HAYDEN, SISTER M. VICTORIA: 368-374
Hedyotis **nicobarensis** 109
Hedyotis procumbens, Typification of and a variety in southeastern United States (Rubiaceae), 377-378; var. **hirsuta** 378
Hibiscus **luteus** 114
HUANG, TSENG-CHIENG; Two new species of Daphniphyllum 28-31
HUNTER, GORDON E.: Revision of Mexican and Central American Saurauia (Dilleniaceae) 47-89
Ilex discolor var. **lamprophylla** 376
Inga, A new species of (Leguminosae) from Panama 377; Central American and West Indian species of (Leguminosae) 265-359; economic importance 273; geography 271; infrageneric categories 276; morphology 267; speciation 277; taxonomy 279; vernacular names 275; sect. Bourgonia 281; sect. Inga 289; sect. Leptinga 344; ser. **Acuminata** 313; ser. Calocephalae 317; ser. **Densiflorae** 302; ser. Dysanthae 320; ser. **Goldmanianae** 319; ser. Inga 328; ser. Leptanthae 312; ser. **Multijugae** 297; ser. **Pilosulae** 314; ser. **Punctatae** 289; ser. **Spectabiles** 322; ser. Tetragonae 324; ser. Vulpinae 323; acuminata 313; **allenii** 346; barbourii 308; belicensis 287; brenesii 330; brevipedicellata 295; calderoni 311; coclensis 343; cookii 312; coruscans 287; davidsoniae 307; densiflora 303; dominicensis 296; edulis 333; fagifolia 283; goldmanii 319; hayesii 316; heterophylla 349; hintonii 310; ingoides 342; jinicuil 353; latibracteata 334; latipes 294; longispica 283; marginata 281; martinicensis 294; micheliana 305; **mortoniana** 351; mucuna 317; multijuga 298; oerstediana 330; paterno 350; pauciflora 329; pezizifera 288; pilosula 314; pinetorum 297; portobellensis 346; punctata 290; quaternata 347; ruiziana 301; saffordiana 354; spindoides 325; schiediana 304; skutchii 300; spectabilis 322; **squamigera** 306; standleyana 321; stenophylla 307; **tenuipedunculata** 308; thibaudiana 299; tonduzii 324; **tysonii** 377; umbellifera 345; venosa 318; venusta 316; vera 335, subsp. **eriocarpa** 338, subsp. **spuria** 339, subsp. vera 336; yunckeri 293
Iridaceae, Chromosome numbers of 103
Kansas, the genus Erythronium (Liliaceae) in 197-204
Leguminosae, A new species of Inga from Panama 377; A new species of Platymiscium from Panama 105; Central American and West Indian species of Inga 265-359
LEÓN, JORGE: Central American and West Indian species of Inga (Leguminosae) 265-359

LEWIS, WALTER L.: Addendum: Schlechter's New Guinea duplicates of Liparis (Orchidaceae) at the Missouri Botanical Garden 259-260; Chromosome numbers of Oldenlandia corymbosa (Rubiaceae) from southeastern Asia 257-258; Arcytophyllum laricifolium (Cav.) Lewis (Rubiaceae) 110; Chromosome numbers of phanerogams 1. 100-103; Claytonia caroliniana var. spatulifolia (Salisbury) Lewis (Portulacaceae) 258-259; Hedyotis nicobarensis Lewis (Rubiaceae) 109; The Asian genus Neanotis nomen novum (Anotis) and allied taxa in the Americas (Rubiaceae) 32-46; Typification of Hedyotis procumbens (Rubiaceae) and a new variety from southeastern United States 377-378

LEWIS, WALTER H. and ROYCE L. OLIVER: Convolvulus rozynskii (Standl.) Lewis and Oliver (Convolvulaceae) 110 Liliaceae, the genus Erythronium in Kansas 197-204 Liparis (Orchidaceae), addendum: Schlechter's New Guinea duplicates at the Missouri Botanical Garden 259-260 Machaonia, new species (Rubiaceae) from Panama 105; **tysonii** 106

Malvaceae, Pavonia (Peltaea) trinervis (Presl) A. Robyns 113-114; Hibiscus luteus (Rolfe) L. O. Williams & A. Robyns 114

McDANIEL, SIDNEY: Three lost species of Piper (Piperaceae) 378-379

Mesechites **pilosissima** 260

Mexican, and Central American, revision of Saurauia (Dilleniaceae) 47-89

Monotropaceae, and Pyrolaceae, pollen morphology and classification of the 213-219

Neanotis, nomen novum (Anotis), the Asian genus and allied taxa in the Americas (Rubiaceae) 32-46, 34; palynological procedures and materials 45; sect. **Patzea** 37; **boerhaavioides** 37; **calycina** 37; **carnosa** 37; **decipiens** 37; **foetida** 38; **formosana** 38; **gracilis** 38; **hirsuta** 38, var. **glabricalycina** 38, var. **glabrior** 38, var. **yakusimensis** 38; **hondae** 38; **indica** 38, var. **affinis** 39, var. **deltoidea** 39; **ingrata** 39; **kwangtungensis** 39; **lancifolia** 39; **longiflora** 39; **monosperma** 39; **montholoni** 39; **nummularia** 39; **nummulariformis** 39; **oxyphylla** 39; **prainiana** 40; **quadrilocularis** 40; **rheedei** 40; **richardiana** 40; **ritchiei** 40; **thwaitesiana** 40; **trimera** 40; **urophylla** 40; **wightiana** 40, var. **compressa** 40

New Guinea, addendum: Schlechter's duplicates of Liparis (Orchiadaceae) at the Missouri Botanical Garden 259-260

NICHOLS, H. WAYNE, JOHN E. RIDGEWAY, and HAROLD C. BOLD: A preliminary ultrastructural study of the freshwater red alga Compsopogon 17-27

North American and Central American, revision of the hexandrous species of Aristolochia 115-196

NOWICKE, JOAN W.: Pollen morphology and classification of the Pyrolaceae and Monotropaceae 213-219

Oldenlandia corymbosa (Rubiaceae) from southeastern Asia, chromosome numbers of 257-258

OLIVER, ROYCE L.: Chromosome numbers of phanerogams 1. 100-103; 110

Orchidaceae, addendum: Schlechter's New Guinea duplicates of Liparis at the Missouri Botanical Garden 259-260

Palicourea **lusinaturalis** 106

Panama, Bernoullia Oliv., a genus of Bombacaceae new to 112; a new species of Inga (Leguminosae) from 377; a new species of Platymiscium (Leguminosae) from 105; new species of Coussarea, Machaonia, and Psychotria (Rubiaceae) from 105-109; Piper and Peperomia (Piperaceae), new to 261-264; two new species of Gloeospermum (Violaceae) from 110-112

Panamanian, notes on Coussarea species (Rubiaceae) especially the 368-374

PARKER, BRUCE C. and JOHN BLECK: A contribution to the ecology of Pelagophycus 1-16

Pavonia trinervis 114

Pelagophycus, a contribution to the ecology of 1-16; laboratory cultivation of zoospores and gametophytes of P. giganteus 11; measurements of growth and developments 4; measurements of light and temperature 7; preliminary studies and establishment of experimental plots 2; transplanting of P. porra juvenile sporophytes to Long Point 10

Peperomia, new species from Ecuador 380; new species from Peru (Piperaceae) 384; species new to Panama 263-264; **ebingeri** 263; philipsonii var. **panamensis** 264; **thienii** 380; **woytkowskii** 384

Peru, Mesechites pilosissima Woodson (Apocynaceae) new to 260-261; new species of Piper and Peperomia (Piperaceae) from 381-384

PFEIFER, HOWARD W.: Revision of the North and Central American hexandrous species of Aristolochia (Aristolochiaceae) 115-196

Phanerogams, chromosome numbers of 1. 100-103

Piper, new species from Ecuador 379; new species from Peru (Piperaceae) 381-383; species new to Panama 261-263; three lost species of (Piperaceae) 378-379; **boquetense** 261; **cajarmarcanum** 382; **dodsonii** 379; **dukei** 262; **mazamariense** 381; **nebuligaudens** 379; **payanum** 262; **pilosissimum** 383; **sternii** 263; **subbrunneispicum** 382; Piperaceae, new from Ecuador 379-381; new species of Piper and Peperomia from Peru 381-384; Piper and Peperomia new to Panama 261-264; three lost species of Piper 378-379

Pithecellobium **gigantifoliolum** 355

Platymiscium, a new species of, from Panama (Leguminosae) 105; **darienense** 105

Poinsettia, the genus in Florida (Euphorbiaceae) 375-376

Portulacaceae, chromosome numbers of 100; Claytonia caroliniana var. spatulifolia (Salisbury) Lewis 258-259; taxonomic status of Claytonia rosea and C. lanceolata 205-212

Psychotria, new species of, from Panama, (Rubiaceae) 105; **cerroazulensis** 107; **quiinifolia** 108; **victoriae** 108; Pyrolaceae and Monotropaceae, pollen morphology and classification of the 213-219

Ridgway, John E.: 17-27

Robertson, Kenneth R.: The genus Erythronium (Liliaceae) in Kansas 197-204

Robyns, Andre: Bernoullia Oliv., a genus of Bombacaceae new to Panama 112-113; Pavonia (Peltaea) trinervis (Presl) A. Robyns (Malvaceae) 113-114; The publication date of the genus Cochlospermum (Cochlospermaceae) 113; Two new species of Gloeospermum (Violaceae) from Panama 110; 114

Rosaceae, chromosome numbers of 100

Rubiaceae, Arcytophyllum laricifolium (Cav.) Lewis 110; Chromosome numbers of Oldenlandia corymbosa from southeastern Asia 257-258; chromosome numbers of 102; Dukea, a new genus of the (tribe Mussaendeae) 360-367; Hedyotis nicobarensis Lewis 109; Notes on Coussarea especially the Panamanian species 368-374; The Asian genus Neanotis nomen novum (Anotis) and allied taxa in the Americas 32-46; Typification of Hedyotis procumbens and a new variety from southeastern United States 377-378

Sarcorhachis sydowii var. **hirsuta** 380

Saurauia, revision of Mexican and Central American (Dilleniaceae) 47-89; geography and paleobotany 54; limits of variation 48; systematic position 56; systematic treatment 57; ser. Gymnogynae 58; ser. Gynotrichae 63; ser. Oreophilae 68; ser. Laevigatae 80; angustifolia 80; aspera 73; comitis-rossei 61; conzattii 77; kegeliana 82; laevigata 84; leuocarpa 82; oreophila 71; pedunculata 78; pittieri 59; pringlei 70; **pustulata** 63; rubiformis 60; scabrida 69; seibertii 81; selerorum 74; serrata 78; **squamifructa** 65; veraguasensis 64; villosa 58; waldeimia 67; zahlbruckneri 72

Skvarla, John J. and B. L. Turner: Systematic implications from electron microscopic studies of Compositae pollen—a review 220-256

Turner, B. L.: 220-256

United States, typification of Hedyotis procumbens (Rubiaceae) and a new variety from southeastern 377-378

Violaceae, two new species of Gloeospermum from Panama 110-112

West Indian, and Central American species of Inga (Leguminosae) 265-359

Wiens, Delbert: 205-212

Williams, Louis O. and André Robyns: Hibiscus luteus (Rolfe) L. O. Williams and A. Robyns, comb. nov. (Malvaceae) 114

Woodson, Robert E., Jr.: Mesechites pilosissima Woodson (Apocynaceae) new to Peru 260-261

Yuncker, T. G.: New Piperaceae from Ecuador 379-381; New species of Piper and Peperomia (Piperaceae) from Peru 381-384; Piper and Peperomia (Piperaceae) new to Panama 261-264

CONTENTS

Central American and West Indian species of *Inga* (*Leguminosae*), by JORGE LEÓN 265-359

Dukea, a new genus of the *Rubiaceae* (Tribe *Mussaendeae*), by JOHN D. DWYER 360-367

Notes on *Coussarea* (*Rubiaceae*), especially the Panamanian species by JOHN D. DWYER 368-374

NOTES 375-384

The genus *Poinsettia* (*Euphorbiaceae*) in Florida 375-376. *Ilex discolor* var. *lamprophylla* (Standl.) Edwin, stat. nov. (*Aquifoliaceae*) 376-377. A new species of *Inga* (*Leguminosae*) from Panama 377. Typification of *Hedyotis procumbens* (*Rubiaceae*) and a new variety from southeastern United States 377-378. Three lost species of *Piper* (*Piperaceae*) 378-379. New *Piperaceae* from Ecuador 379-381. New species of *Piper* and *Peperomia* (*Piperaceae*) from Peru 381-384.

General Index for Volume 53, 1966 385-388